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The impact of native and exotic plants on soil biodiversity and ecosystem function

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The impact of native and exotic plants on soil biodiversity and ecosystem function

A selection of UK Collembola

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Abstract

Soil biodiversity is an often overlooked component of global biodiversity, despite being important for supporting soil ecosystem services, notably decomposition processes. As the UK becomes increasingly urbanised, knowledge is required to help gardeners maximise urban green space resources for biodiversity. It is often assumed that non native vegetation has negative impacts on biodiversity, however, this hypothesis has not been tested for soil biodiversity. The overarching aims were to establish whether the geographical origin of vegetation affected soil faunal assemblages and decomposition rates for a UK soil. Traditional taxonomic methods and a molecular phylogenetic approach were used to characterise the Collembola communities of plots planted with vegetation from three geographical regions: 'Native', 'Near native' and 'Exotic'. For comparison, additional soil cores were collected from the amenity grassland sites adjacent to the experimental plots, a lowland heath and a semi-natural woodland. No difference was found either in terms of the taxonomic diversity (1-D & H') or phylogenetic diversity (PD & MPD) for the Collembola, under the different vegetation treatments, although differences in abundance were observed for some taxa (Acari & Collembola). Decomposition rates were assessed for each plot, using both twig (*B. pendula*) and leaf (*Q. robur*) litter bags for the soil mesofauna and bait lamina strips for earthworm activity; none of these parameters showed evidence of a vegetation origin effect on decomposition processes. The greatest differences were found when all sites were considered, with distinct Collembola communities found at each of the habitats; the semi-natural habitats had greater Collembola species diversity than the experimental plots, however, the decomposition rates of the latter were significantly higher. The implications of all results have been discussed with regards to the management of gardens for soil biodiversity, reaching the conclusion that vegetation origin is not of paramount importance.

Contents

Dedicated to Maisie Lilian Udall
(May 1919 - April 2011)

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Chapter 1. Literature review and project introduction

1.1. Introduction

Terrestrial environments, especially in the United Kingdom, are becoming increasingly urbanised (Home 2009), a process which threatens soil integrity and biodiversity (Goddard et al. 2010). Soil biodiversity is still a relatively overlooked and understudied component of global biodiversity (Decaëns 2010; André et al. 2002) despite underpinning the provision of many ecosystem services (Daily 1997), some of which become increasingly important with urbanisation (Bolund & Hunhammar 1999). The public spaces and private gardens, known as urban green space, have been seen as a 'Panacea' for urban biodiversity conservation (Goddard et al. 2010). More work is needed; Davies et al. (2009) identify that knowledge regarding management practises, specifically information on how to maximise the resources provided by urban green spaces to promote biodiversity, is lacking. What is certain is that gardens can represent a valuable refuge for native biodiversity; combined they comprise an estimated 430,000 ha: 2% of land area in the UK (Davies et al. 2009). With this in mind, it is clear that gardeners planting preferences could be of great importance, affecting wider UK biodiversity. Decisions over which plants to grow are faced by both town planners and gardeners, with high proportions (59%-70%) of the plant species grown in gardens and urban areas not native to the UK (Owen 1991; Thompson et al. 2003; Loram et al. 2008). It is not fully known what effect this inclusion of exotic flora is having on native faunal biodiversity, in particular soil faunal biodiversity.

Before providing an overview of the concepts and relevant literature it is useful to first discuss the relevant terms. In the light of this, this review is structured as follows: the

definitions of biodiversity (Section 1.2.) and soil biodiversity (Section 1.3.) are explored, before the literature pertaining to gardens and biodiversity is reviewed (Section 1.4.). The variety of methods available to explore and characterise biodiversity is discussed (Section 1.5.) and the role of soil biodiversity in ecosystem function is introduced (Section 1.6.) with some of the factors known to mediate soil fauna distribution mentioned (Section 1.7.). Sections 1.8. and 1.9. present the background to vegetation origin and the question of its importance. This is followed by a brief introduction to the 'Plants for Bugs' project (Section 1.9.1.) and finally, the aims of this PhD and its position within the 'Plants for Bugs' project are set out (Section 1.10.).

1.2. What is biodiversity?

The terms 'biodiversity' and 'biological diversity' are used interchangeably, to convey the same concept, with the former being a contraction of the latter. In 1992, The Convention on Biological Diversity defined biodiversity as '*the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems*' (United Nations 1993). Although this definition does cover all terrestrial ecosystems and their biological diversity, the study of soil biodiversity is often overlooked in experimental and survey work (André et al. 2002; Parker 2010). This aspect of global biodiversity is an important component both in supporting and regulating a range of ecosystem services. Soil ecosystems are responsible for processes including the regulation of decomposition and nutrient cycling (nutrient mineralisation) which are necessary for vegetation growth and provide a basis for many ecosystems (Daily 1997; Board of the Millennium Ecosystem Assessment 2005). It is the functional

integrity and stability of an ecosystem that determines the quality of the services supplied (Tilman 1997; Hooper et al. 2005).

Besides the ecosystem supporting and regulating service justifications for protecting biodiversity, its conservation is also important as it represents a safeguard to maintaining a genetic library for the future (Myers 1997). There are many other reasons for protecting biodiversity, on which it is difficult to place quantified valuations, for example; aesthetic enjoyment and cultural values (Kumar & Kumar 2008). Even if it is found that exotic plants cause reductions in soil biodiversity with no resulting impact on ecosystem function, due to for example functional redundancy, there are still compelling moral obligation arguments to conserve as much as we can for as long as possible (Hampicke 1994). Additionally there is the precautionary principle; as the impact of removing biodiversity components on ecosystem function is not known, they should be protected in case alteration results in irreversible damage (Arrow & Fisher 1971).

The designation and prioritisation of conservation areas is often dependent on measures of biodiversity; 'biodiversity hotspots' are used to identify areas of conservation value (Myers et al. 2000). However, in a survey of three major conservation journals: Biodiversity and Conservation, Biological Conservation, and Conservation Biology, only 8% of the articles dealing with animal taxa dealt with soil fauna, since an estimated 25% of living described species reside within the soil and the litter immediately above, this is a large discrepancy (Decaëns et al. 2006). This bias is also reflected in IUCN and CITES conservation directives (Decaëns et al. 2006).

Soil biodiversity is not unthreatened; both the spread of urban development and agricultural practises, such as tilling, jeopardise soil ecosystem integrity (Gardi et al. 2009; Parker 2010). Before conservation is undertaken the biodiversity present needs to be known and any conservation requirements assessed (Gardi et al. 2009); it has been observed that there is a dearth of information on soil organisms especially at the scale that is required by conservation planners (Parker 2010). It is often cited that impediments to the study of soil biodiversity lie in the lack of expertise and resulting decreased taxonomic resolution compared to that of other fields (e.g. André et al. (2002), Rougerie et al. (2009)) as well as the labour intensive nature of morphological identifications (Wu et al. 2009) and inefficient or biased sampling methodologies (André et al. 2002).

1.3. Soil biodiversity

The biodiversity of soils is often several orders of magnitude greater than that found aboveground (Heywood 1995) with this species richness being attributed to the heterogenous nature of the soil habitat (Bardgett 2002). Soils have been described as 'treasure-troves' of biodiversity (Parker 2010) and "the poor man's rainforest" (Giller 1996) with estimates showing that approximately 50% of total animal biomass is found below ground level (Fierer et al. 2009). Additionally soil faunal biomass has been estimated at 2% of that of the microbial biomass across a range of biomes (Fierer et al. 2009). It is likely that the vast majority of even some of the larger components of the soil fauna such as soil microarthropods remain incompletely described (André et al. 2002; Rougerie et al. 2009). The percentage of undescribed species has been estimated at upwards of 90% (André et al. 2002). Even in well sampled regions it is proposed that a maximum 10% of soil microarthropod populations have been studied (André et al. 2002).

So despite acknowledgements of its importance, it can be seen that soil biodiversity is still an overlooked constituent of global biodiversity.

The soil fauna are separated into groups based on width: microfauna (diameter less than 100 µm), mesofauna (diameter between 100 µm and 2 mm) macrofauna (diameter between 2 mm and 20 mm) and megafauna (diameter greater than 20 mm) (Bardgett & Cook 1998; Coleman & Wall 2007). The macrofauna and megafauna are sometimes lumped together as soil organisms with a diameter greater than 2 mm (Turbé et al. 2010). There is some overlap in these size classifications due to the variation in size of the different species and different instars (Coleman & Wall 2007; Decaëns 2010).

1.3.1. Microfauna

The main constituents of the microfauna are the nematodes and the protozoa (Petersen & Luxton 1982; Cole et al. 2006; Coleman & Wall 2007), although Petersen & Luxton (1982) also include the larger Tardigrades (waterbears). Within the soil profile microfauna travel through pores created by larger soil organisms; the macrofauna.

Nematodes have a range of feeding types, in ecological studies whole families are often allocated functional groups based on their feeding behaviour and associated morphological adaptations (Petersen & Luxton 1982; Yeates et al. 1993; Bongers & Bongers 1998) thereby facilitating their study (e.g. Bardgett & Cook (1998)). Both the micro- and mesofauna have indirect impacts on the decomposition processes enhancing nutrient mineralisation; they influence fungal growth and activity via grazing behaviour and have been found to passively transport microorganisms in their guts (Griffiths & Bardgett 1997; Coleman & Wall 2007). Enhancement of nitrogen mineralisation has been

observed where bacterial feeding nematodes and microarthropods (see below, e.g. Collembola) were both present (Bardgett & Chan 1999).

1.3.2. Mesofauna

The mesofauna group encompasses a range of microarthropods: Acari (mites), Collembola (springtails), Tardigrades (waterbears), Pauropoda and Protura as well as the Enchytraeidae (pot worms, Annelida) (Cole et al. 2006; Coleman & Wall 2007). Mesofauna components are often studied due to their high abundance in soils and greater ease of identification compared to the microfauna.

The Collembola are a Class of Hexapod (Regier et al. 2010), most closely related to the Protura (Misof et al. 2014), they are an important component of the mesofauna and can be used as a tool to look at differences in biodiversity between experimental treatments.

Collembola are often studied due to their abundance in soil ecosystems and their ubiquity and dominance across a range of ecosystems, from olive groves in North-Eastern Portugal (Gonçalves & Pereira 2012), to teak forests and fallow paddy fields in Java (Widyastuti 2004). Collembola are commonly found in the soil and are also present in a variety of habitats and ecosystems ranging from leaf litter to the canopy of trees (Hopkin 2007). The Collembola and Acari are two of a handful of terrestrial arthropod groups to be found in the continental Antarctic region (e.g. Sinclair et al. (2006) and Greenslade (1995); the others being the Chironmidae (Diptera) and Ceratophyllidae (Siphonaptera) (Usher & Edwards 1984).

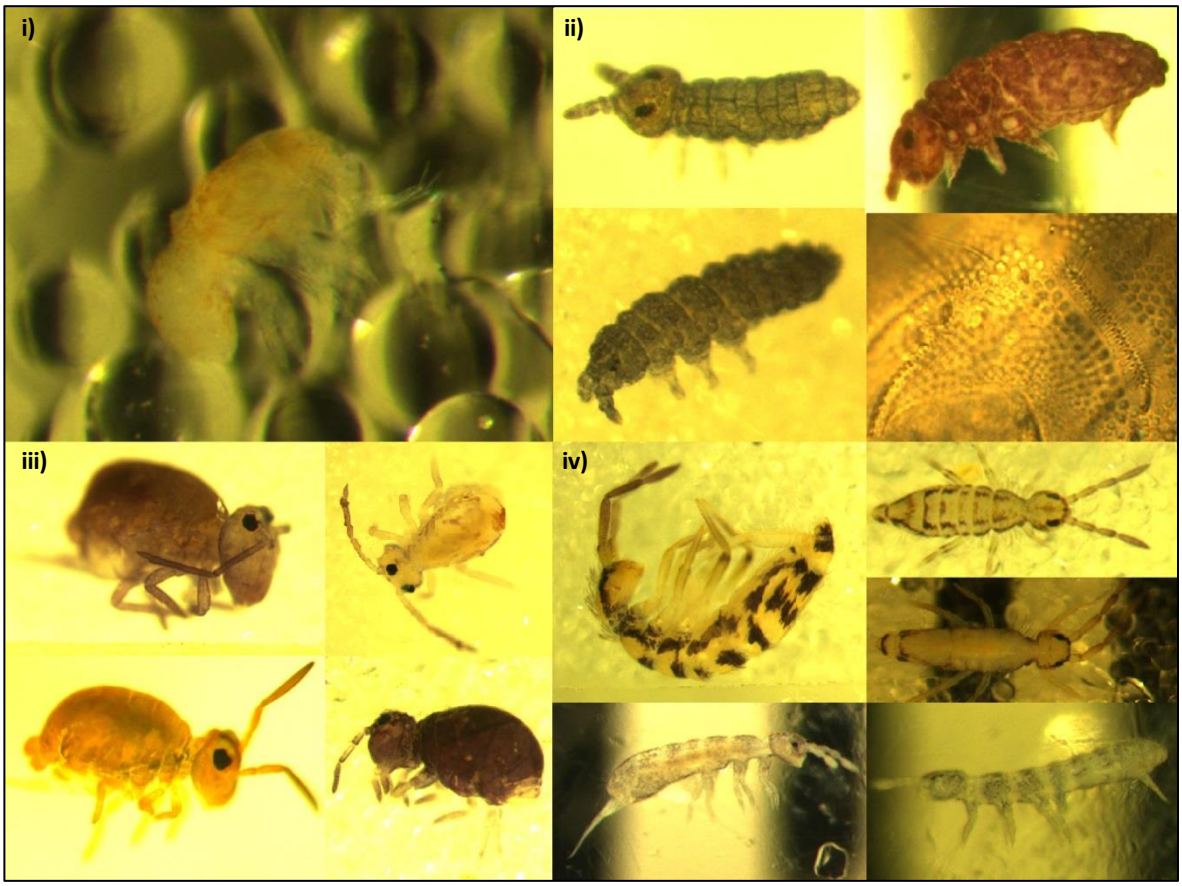

Figure 1.3.2. A selection of UK Collembola, with species representing the four Orders, **i**) Neelipleona, **ii**) Poduromorpha, **iii**) Symphypleona, and **iv**) Entomobryomorpha.

Worldwide there are approximately 6,500 - c 7,000 described Collembola species (Hopkin 1997; Deharveng 2004) whilst in the UK Hopkin (2007) recognises 250 species, although others are almost certainly present: approximately 380 spp. (Peter Shaw, pers. comm., 2015), see Figure 1.3.2. for images of a selection of the UK species.

In the first national UK survey of soil invertebrates, a component of the Countryside Survey 2000 (CS2000); an 'audit' of the UK's natural resources, it was again confirmed that the Acari and the Collembola are dominant taxa as they were recorded in 94% and 78% of samples, respectively (Black et al. 2003). This was based on 1052 samples collected from a range of soil types, under a variety of vegetation classifications taken from across Great Britain. It is rare, however, that studies focus on identifying both the Collembola and the Acari; in a review of the literature André et al. (2002) found that the

Collembola were the most frequently studied soil mesofauna taxon followed by Oribatid mites.

The Environmental Assessment of Soil for Monitoring (ENVASSO), an EU consortium set up to establish a standardised soil monitoring system with the aim of protecting EU soils, have also identified the Collembola along with the Enchytraeidae as being components of the mesofauna for which monitoring priority should be allocated; they were given a level 1 priority for the key issue of species diversity with the expectation that they could provide an indication of any decline in overall soil biodiversity (Jones et al. 2008). Gardi et al. (2009) suggest that ideally all soil organisms should be assessed, but that given practical considerations, the ENVASSO level 1 ecosystem elements should be the minimum level of assessment. In a study of land use change and grassland succession by Chauvat et al. (2007) it was noted that changes were observed earlier in the Collembola than for either Oribatid mites or ants (Hymenoptera: Formicidae), so this makes them a good organism to study in the early stages of field experiments and early indications of change.

Assigned to either the detritivore or herbivore functional group, Collembola fulfil an important role as members of decomposer communities (Petersen & Luxton 1982; Hopkin 1997; Filser 2002). In microcosms (Shaw 1988) and soil ecosystems (Griffiths & Bardgett 1997) they have been found to selectively graze on fungal hyphae mediating the distribution, abundance and activity of the soil microorganisms which facilitate nutrient mineralisation.

The soil mesofauna are not uniformly distributed through the soil profile; Collembola abundance varies with depth (Berg et al. 1998) and different species are adapted to living at different depths (Hopkin 1997). Following Gisin (1943) they can, and often are, divided into life-form groups based on morphological characters with differing physiological and ecological characters. These are: epiedaphic, found on the soil surface and in the leaf litter layer; euedaphic, within the soil profile and hemiedaphic, intermediate between the morphological and physiological characters associated with the previous two groups (Lavelle & Spain 2005). Euedaphic Collembola often have a reduced furca and there are other differences e.g. cuticle structure between the groups (Nickerl et al. 2012).

1.3.3. Macrofauna

The soil macrofauna classification contains the Annelids: (earthworms), Myriapods: Chilopoda (centipedes) Diplopoda (millipedes), Oniscidea (woodlice) and Formicidae (ants). It is the macrofauna that are considered ecosystem engineers as they have more direct effects on soil structure than the micro or mesofauna (Jones et al. 1994). Being larger they are more mobile and so are better at mixing the plant material into the soil profile and creating burrows (Jones et al. 1994; Cole et al. 2006; Coleman & Wall 2007).

In a long-running soil ecosystem study at Sourhope, in Scotland, the macrofauna were found to have greatest impact on soil properties, probably due to the inclusion of earthworms within this functional group (Cole et al. 2006). Earthworms improve soil aggregation and soil porosity affecting water movement and drainage; their activity creates soil pores which result in zones of preferential flow of water, enhancing water infiltration whilst also reducing water run-off (Lavelle et al. 2006). Earthworm casts, the soil ingested and excreted by earthworms, alter soil structure increasing water retention.

Macrofauna community patterns have also been proposed as the basis for indicators of soil quality e.g. Nuria et al. (2011). In the macrofauna size class ENVASSO selected the earthworms as 'key indicators' to which monitoring priority should be given to alert specialists to possible declines in overall soil biodiversity (Jones et al. 2008). Many of the other macrofauna organisms found within the soil (Diptera, Coleoptera etc.) are only transiently present at certain larval stages and at abundances that are often too low for statistical analysis compared to other elements of the soil fauna (e.g. the Collembola) which are more permanent and abundant soil dwellers (Coleman & Wall 2007).

1.4. Gardens and biodiversity

In the UK an estimated 87% of households have access to a garden (Davies et al. 2009). Gardens, as defined by Gaston et al. (2005), are the '*private spaces adjacent to or surrounding dwellings, which may variously comprise lawns, ornamental and vegetable plots, ponds, paths, patios, and temporary buildings such as sheds and greenhouses*'. In a survey into gardening behaviours, commissioned in 2003 by the Royal Horticultural Society (RHS) of those who had a garden (83% of interviewees), 77% were interested in gardening and of these gardeners over half already had measures in place to attract wildlife (i.e. bird feeders), whilst over a quarter expressed a wish to 'actively encourage all wildlife' (MORI 2003). There has also been an increased emphasis in the media on biodiversity, both in a global and an urban context, resulting in a more biodiversity conscious public accompanied by popular science books offering advice on gardening for wildlife (e.g Thompson (2006) and Tait (2006)). Despite the role of earthworms in compost heaps often being mentioned, soil biodiversity is not the focus of these guides. However, there has been a relatively recent research programme into the biodiversity

and function of soils based on an observed '*background of increasing interest in soil biodiversity'* (Usher et al. 2006).

There have been previous studies into the biodiversity of urban green spaces including gardens. The longest running published survey of garden biodiversity was conducted by Jennifer Owen over a 30 year period, between 1972 and 2001, in an urban domestic garden in Leicester (Owen 1991; Owen 2010). A variety of sampling methods were used to capture and record 1,723 invertebrate species in the first 15 years, rising to 2,135 invertebrates by the end of the study, an estimated quarter of the UK's phytophagous insect species. However, this figure did not include data on the main constituents of soil biodiversity. It was noted that Collembola were commonly present, however, abundances were not recorded and no species were identified (Owen 1991).

This work provided a starting point for further research by the Environment and Biodiversity Research Group at the University of Sheffield. Between 2000 and 2002, inclusive, a set of Sheffield based surveys; Biodiversity of Urban Gardens in Sheffield (BUGS I) (Thompson et al. 2003; Gaston et al. 2005; Thompson et al. 2004; Gaston et al. 2005; Smith et al. 2005; Smith et al. 2006; Thompson et al. 2005; Smith, Gaston, et al. 2006; Smith, Thompson, et al. 2006) were conducted to explore both the floral and invertebrate biodiversity of gardens and the conservation resources found therein. This was followed in 2004-2007 with a second set of closely related studies expanded to look at gardens from across the UK (BUGS II) (Loram et al. 2007; Gaston et al. 2007; Loram et al. 2008; Smith et al. 2010; Davies et al. 2009). Although they both examine a range of invertebrate taxa, the impact of the variables chosen for this study, specifically that of plant origin (native/exotic), and its impact on soil biodiversity was unexplored.

It has been suggested that on a landscape scale gardens can help to link fragmented green spaces in urban areas providing corridors of connectivity and enhancing networks for biodiversity (Rudd et al. 2002; Goddard et al. 2010). Davies et al. (2009) estimated the resources already offered by gardens to biodiversity, but focussed predominantly on those provided for birds (supplementary food and nest boxes) and habitat features such as ponds, whilst BUGS I (Gaston et al. 2005) also included testing some of the recommendations for increasing habitat suitability for certain invertebrate taxa. These studies included ponds, nettle patches for Lepidoptera larvae, dead wood for saproxylic organisms and fungi, and nest sites for Hymenoptera with a varying degree of success observed in attracting and increasing biodiversity. These studies lacked any investigation or full discussion of implications for soil biodiversity. High soil biodiversity has been observed in gardens; Widyastuti (2004) conducted a study comparing garden soil biodiversity to nearby habitats (teak forest and paddy fields) encountering the highest abundances and species diversity at a garden site. However, this study was located in Indonesia where the climate is different to that of the UK and was conducted without the intention of testing plant origin, though some observations were made with respect to vegetation cover and soil moisture no data was provided to support the authors assertions.

1.5. Characterisation and measurement of soil biodiversity

In order for the progress of conservation efforts to be assessed, the initial level of biodiversity present has to be identified and then monitored (Gardi et al. 2009). Species are not distributed evenly across the globe and communities vary in their diversity and the abundances of their constituent taxa. André et al. (2002) and Chauvat et al. (2007) both note that it is important to look at more than one taxon when conducting soil

ecosystem studies. Ideally as many soil fauna groups as possible should be explored, although it is seldom practical, given the constraints of knowledge and time, to assess all. There are a variety of approaches to assessing biodiversity which all measure properties of community structure such as the abundance of taxa as well as species diversity and functional diversity.

1.5.1. Abundance and biomass

Abundance is a simple measure that is often used for monitoring biodiversity and is the number of individuals of a selected species, taxonomic group or functional group present in an area. The use of abundance as a measure minimises identification efforts as only the taxon of interest need be identified. Abundance data are frequently used in soil biodiversity studies (e.g. Cole et al. 2006) and can easily be converted to give density figures i.e. abundance per unit of substrate mass, m-2 (standard), or per unit volume (e.g. for suspended soils) (Rusek et al. 2000).

In the national survey of soil invertebrates, conducted for CS2000, soil biodiversity was characterised using basic methods of assessment. The soil microbial distributions were assessed by culturing soil of a known dry mass on agar and determining abundance estimates by counting the number of viable cells after a controlled incubation period (Black et al. 2003). For the other chosen taxonomic groups (Collembola and Acari) analysis was restricted to the comparison of percentage occurrences in the samples under each condition. Only the number of species of Oribatid mites per sample were explored separately (Black et al. 2003).

Biomass is material of biological origin, either living or recently living and can be measured by individual or collective dry weight. This is particularly useful for the elements of the soil fauna where individual identification is not feasible as it treats soil biota as a singular entity. Measurements or estimates for microbial biomass are particularly common (e.g. Fierer et al. (2009)).

1.5.2. Diversity

Hill (1973) defines the species diversity of a community or dataset as '*the inverse of the weighted mean of the proportional abundances*'. There are numerous diversity indices commonly employed to provide metrics for assessment and comparison of biodiversity and the more popular of these are detailed here; see Magurran (2004) for an exhaustive compilation of the remainder. These measures can be roughly divided into those pertaining to species richness and those dealing with heterogeneity or evenness (Whittaker 1972).

There has been recent discussion as to the precise meaning of diversity and which indices can be best used to represent it (Tuomisto 2010; Gorelick 2011; Jurasinski & Koch 2011; Tuomisto 2011). The discussion followed a paper by Jurasinski et al. (2009) highlighting that different authors and studies have used the term diversity to cover a gamut of subtly different concepts and have not distinguished between them. As well as being defined as the number of different species, diversity is also used to convey the species composition and the distinctness of different sites and across different scales (Whittaker 1960; Tuomisto 2010). The term is also often confused with the indices used to measure its different aspects (Jost 2006; Tuomisto 2010; Jurasinski & Koch 2011).

In response to a previous article by Jost (2006), Tuomisto agreed that the effective number of species be categorised under the term 'true diversity', to prevent ambiguity (Tuomisto 2010; Tuomisto 2011) which sounds reasonable, though surely so long as each author makes clear what they mean by diversity then this should not matter? Jurasinski and Koch (2011) also advocate a stricter designation of 'true diversity', however, Gorelick (2011) disagreed on the basis that it implies that other indices are somehow 'false'. How phylogenetic diversity fits into this debate is discussed in Section 1.5.3..

Whittaker (1960) proposed the division of diversity into three spatial levels, each assessing diversity across different landscape scales; alpha, beta and gamma diversity. Whittaker (1960) defined alpha diversity as '*the richness in species of a particular stand or community, or a given stratum or group of organisms in a stand*' and so species richness is one of the simplest measures of alpha diversity. It is a count of the number of species in a sample of standard size of selected area or ecosystem and does not take into account the relative abundances between the species present (Whittaker 1972). This is also referred to as inventory diversity by Jurasinski et al. (2009). This study is primarily concerned with alpha diversity as this is the predominant approach for similar applied ecological studies (Clough et al. 2007).

Absolute species richness (R) may be determined with a fair degree of accuracy where the number of species present is not too numerous and correct identification can be made with reliable accuracy (i.e. for well-known groups such as vascular plants or in small or well studied regions) (Magurran 2004). This is often not the case for soil ecosystems leading diversity to be underestimated (André et al. 2002). The number of species encountered is proportional to a power of the area sampled (MacArthur & Wilson 1967)

and so it is important that where sites are compared they are done so over the same area.

An accurate representation of the real species richness relies on the intensity of sampling as well as species delimitations and the taxonomic expertise available. Species richness can be estimated in order to address the first of these issues using taxon sampling curves. These taxon sampling curves can either be individual-based or sample-based and are either accumulation or rarefaction curves and are used to compensate for the effects of unequal sample size (Gotelli & Colwell 2001). A second aspect of alpha diversity is the pattern of relative importance of the species in the sample, there are several indices that can be used to measure the slope of this evenness (Whittaker 1972).

It is also often informative to compare species richness and community composition between ecosystems or treatments. The change in species composition, known as species turnover, can be calculated to give the degree of community differentiation. The number of species under each condition is determined and then the number of species only found in one or the other of the conditions is worked out. This is termed the beta diversity and provides a measure of local scale biodiversity (Whittaker 1960).

Gamma diversity assesses species richness across a greater spatial scale, it is a more regional assessment of diversity, utilising the species diversity of a number of community samples from a range of environments (Whittaker 1960).

Two of the most widely used diversity indices are the Shannon-Weiner index and the Simpson index, see Table 1., Appendix 1.5.2., for equations. The Shannon-Wiener index

(H'), also called Shannon entropy (and sometimes mislabelled as the Shannon-Weaver index (Spellerberg & Fedor 2003)), is probably the most prevalent diversity index and was put forward by Shannon (1948) in the context of information theory, building on the work of Wiener in the late 1940's. It measures the average level of uncertainty in predicting the identity of the next randomly picked species and can be used to calculate species evenness; it is based on the sum of the weighted proportional abundances of each species in a sample. This method does have pitfalls; it is more sensitive to the presence of rare species, so it is important that all components are represented in the sample as omitted species at low abundances have a great effect and result in an incorrect H' value (Hill 1973; Magurran 2004). Interpretation and visualisation can also be difficult as it is calculated using logarithms (Hurlbert 1971; Hill 1973) and authors may differ as to which log base is used, making results difficult to compare.

The Simpson index (D) is also a well-known index of species diversity; Magurran (2004) called it '*one of the most meaningful and robust diversity measures available*' whilst describing the general preference for the Shannon-Wiener index as 'inexplicable'. This measure was first published in an ecological context by Simpson (1949) and calculates the probability that two randomly drawn individuals will be of the same taxon making use of their proportional abundances. It is more sensitive to the numbers of the abundant species and so is considered an indicator of dominance concentration (Hill 1973; Whittaker 1972). It produces a statistic (D) where samples with greater diversities have a smaller value and those that are less diverse have a higher value and so D is sometimes transformed. The inverse can be taken (inverse Simpson index) or it can be subtracted from 1 (Gini-Simpson index) to give the probability that two randomly drawn individuals

belong to different taxa (see Magurran (2004)), this is the commonest form of the index, (see Table 1., Appendix 1.5.2.).

Within the soil biodiversity literature both of the indices above have been used; the Shannon index (e.g. Cole et al. (2006)) and the Simpson index (e.g. Shaw (2003)) have been used to assess communities and differences in species compositions between sites or treatments and frequently more than one index has been employed in each study (e.g. Chauvat et al. (2003) in the study of successional changes in Collembola community structure).

1.5.3. Phylogenetic diversity

Traditionally the methods employed to investigate the diversity of soil fauna involve extraction of soil organisms and their classification followed by comparison using the metrics above to assess alpha, beta and gamma diversity. This treats all the species as evolutionarily independent (Swenson et al. 2012) and does not take phylogenetic relationships into account (Gorelick 2011). Species to genera ratios have been used as far back as 1946 in the comparison of ecological community structure (Elton 1946) although Magurran (2004) traces back the beginning of the search for ways to measure taxonomic diversity to Pielou (1975). This paper stated that communities where species are divided over many genera will have greater diversity than those where the same number of species are found to belong to fewer genera or the same genus (Pielou 1975). To give a simplified and extreme example; a collembolan community of four different species of *Entomobrya* would encompass less genetic diversity than a community with one *Entomobrya*, a Neelid, a Symphypleona and a Poduromorpha despite both communities

having the same alpha diversity at the species level. This illustrates the difference between species richness and taxonomic or phylogenetic diversity.

Pielou (1975) and subsequent authors (e.g. Izsák and Papp (2000); Desrochers and Anand (2004)) describe how indices already developed can be adapted so that taxonomic weightings are added to incorporate different levels of taxonomic diversity. Molecular methods are of increasing importance to the study of the diversity of species found in ecosystems (Emerson & Gillespie 2008). The use of DNA sequence data allows the genetic diversity of biological communities to be explored and phylogenetic trees built to reconstruct evolutionary relationships.

Phylogenetic diversity (PD) as a means of quantifying species diversity was first proposed by Faith (1992). It is intended as a method for prioritising conservation efforts to protect areas or choose complimentary areas to maximise the diversity of species conserved. PD is calculated using phylogenetic distances; the sum of the branch lengths between taxa in a tree of phylogenetic relationships. It has been shown that the areas with the greatest phylogenetic diversity are not necessarily those with the greatest species richness (Forest et al., 2007). If the primary aim of conservation measures is to protect biodiversity as a genetic resource then this should be the preferred selection method as it highlights areas containing more phylogenetically diverse species which would be more likely to contain different genes and greater feature diversity (Forest et al., 2007).

Phylogenetic beta diversity (phylobetadiversity) has been developed as a method of incorporating phylogenetic data into the analysis of species turnover between communities (Graham & Fine 2008; Swenson 2011; Swenson et al., 2012). Traits or

habitat characteristics can also then be mapped onto the phylogenies to assess niche conservatism traits (Graham & Fine 2008). Emerson et al. (2011) used these principals in to investigate Collembola community structure across differing geographic scales, revealing the extent of cryptic diversity. This work highlights the need for further taxonomic effort coupled with molecular work if true species diversity is to be assessed and compared. Emerson et al. (2011) also recognised the benefit high throughput parallel sequencing could bring to the construction and comparison of community phylogenies for otherwise taxonomically challenging soil fauna.

1.5.4. DNA derived species boundaries

DNA sequence data is also a valuable tool used to identify and add characters to aid in taxonomic classification (e.g. Regier et al. (2010)). It is also hoped that molecular methods such as DNA barcoding initiatives may also address the recognised taxonomic deficit, helping to survey and identify biodiversity (Hebert et al. 2010; Rougerie et al. 2009). Hebert et al. (2003) evaluated the use of a region of the COI gene on the mitochondrial genome as the basis for a barcode identification system for all animals using Lepidoptera (11,289 individuals from 1327 species) as an example to show the effectiveness with which it can be used to build reference libraries, see Chapter 4., Section 4.1.2. for greater detail. In addition to facilitating identifications it is expected it will ensure newly discovered taxa are placed correctly. Phylogenetic trees built using DNA sequences are used to reconstruct relationships between species, aid in taxa delimitations and have revealed cryptic species (Schneider et al. 2011; Porco et al. 2012).

However, the over-zealous application of a phylogenetic species concept can lead to inflations in species numbers as many molecular-based revisions recommend splitting

(Agapow et al. 2004), this can have repercussions for conservation which is heavily dependent on species lists (Isaac et al. 2004). With this is mind, within the context of soil biodiversity, DNA sequencing has recently been used to uncover hidden diversity even in the seemingly well characterised and widespread collembolan species *Parisotoma notabilis.* Prior to the work by Porco et al. (2012) *P. notabilis* was considered a single, readily identifiable species with homogenous, distinctive morphological characters. However, based on DNA sequences from the COI standard barcode region phylogenetic trees with a polyphyletic *P. notabilis* were produced leading to the proposal that the species is actually comprised of at least four lineages supported by a clear geographical pattern (Porco et al. 2012). Rougerie et al. (2009) also used this region to construct Collembola and earthworm phylogenies which have emphasised the high level of cryptic diversity in these taxa and the need for further taxonomic scrutiny. Molecular approaches using the COI region can also shed light on phylogeographic species patterns for example in a region of the Mediterranean basin Cicconardi et al. (2009) found evolutionarily distinct collembolan lineages persisting across a fine scale, again hinting at currently unrecognised valid species. Similar work has recently been undertaken for the Collembola genus *Entomobrya* contributing to the discussion on morphological/molecular species delimitations for this group (Katz et al. (2015) and Peter Shaw, pers. comm., 2015)).

The study of operational taxonomic units (OTUs), which are DNA sequences grouped above a set threshold of similarity (e.g. 97% (Fierer et al. 2007); 80-100% (Wu et al. 2009)), has been used in assessments of soil microbial diversity. Studies of these taxa are problematic; identifications are difficult due to both the abundances involved and the taxonomic deficit and consequently it is estimated that over 50% of species have not yet been named and described (Pace 1997; Fierer et al. 2007). Fierer et al. (2007) used OTUs

to investigate patterns of community genetic diversity in the archaea, bacteria, fungi and viruses with all groups found to be both globally and locally diverse and the virus lineages present in the soil being distinct from communities sampled in other environments. Wu et al. (2009) used a range of OTU thresholds in a study comparing the community structures of soil fauna obtained from molecular and morphological assessments of taxonomic levels, identifying incongruences in the taxa richnesses identified.

1.5.5. Community structure and functional diversity

The above are measurements of properties of community structure, however, they treat all the taxa as ecologically equivalent (Swenson et al. 2012). Community structure can also be explored using molecular methods. There are other phylogenetic metrics besides PD that can be derived from phylogenetic trees using branch length distances: net relatedness index (NRI) which tests whether a chosen community is phylogenetically clustered or over-dispersed within the regional pool of taxa and the nearest taxon index (NTI) which looks at whether closely related taxa tend to co-occur (Webb 2000; Webb et al. 2002; Webb et al. 2008). These measures were defined and then used by Webb (2000); to assess the community structure and patterns of taxonomic diversity in an Indonesian rainforest and were subsequently further developed by Webb et al. (2002).

Within soil ecosystems, phylogenetic diversity has been used to investigate the effect of community assembly on ecosystem function (Maherali & Klironomos 2007). It has been suggested that this can provide information on the processes that generate observed community structures, as well as the evolutionary dynamics of community assembly (Emerson & Gillespie 2008). These methods could be used to compare the community

structure of soil fauna assemblages under different treatments or in different habitats within the same region.

Functional diversity is a measure of the complementarity or dissimilarity between species (Petchey et al. 2004). In the past, taxa have also been assigned to 'guilds' or 'functional groups' as there are species that fulfil similar roles in ecosystem processes, competing for the same resources and are able to replace each other (Brussaard 1998). Functional group approaches are based on separating taxa according to morphological and behavioural characteristics related to feeding habits, these are readily recognisable and can reduce the taxonomic effort required (e.g. Cummins et al. (2005)). Within soil biodiversity literature, body size has been used as a proxy for functional group classification (Cole et al. 2006) as it has been found to correlate with metabolic rate and food size in addition to generation time and population density (Peters 1983). Brussaard (1998) recommended that the soil fauna are divided into three groups: the 'root biota' which are associated with living plants; the 'decomposers', responsible for regulating the activity and abundances of microbial feeders and other microorganisms, including the microflora, micro and mesofauna; and the 'ecosystem engineers' the meso and macrofauna capable of altering microhabitats.

1.6. Biodiversity in ecosystem function

The ecosystem services provided by urban green spaces have previously been shown to be important, with identified advantages including improved air filtration, microclimate regulation, noise pollution reduction, sewage treatment as well as recreational and cultural benefits (Bolund & Hunhammar 1999; EU 2010). Water cycle regulation is especially important as a large fraction of surfaces in urban areas are tarmacked, paved or

built on, limiting their permeability to rainwater and making them susceptible to flooding (European Union 2010). Ensuring the maintenance of the hydrological properties of the remaining green spaces is therefore important. A functioning ecosystem is necessary for buffering rainwater drainage and can be enhanced by the activity of soil biota and vegetation cover (Bolund & Hunhammar 1999). The contributions to ecosystem processes by soil invertebrates are detailed by Lavelle et al. (2006).

There has been substantial research into the effect of biodiversity (i.e. number of species) on the stability of ecosystems and their functioning (Ives & Carpenter 2007). Ecosystem performance has previously been linked to species diversity (*e.g.* Naeem et al. 1995). It has been hypothesised that greater species diversity means more interactions between trophic levels resulting in greater ecosystem stability (MacArthur 1955). Species which may appear functionally redundant can offer alternative paths for the flow of energy so that there is no interruption or collapse in processes created by gaps in the food chain in the event of disturbances or perturbation e.g. by drought, fire, species loss or invasions by exotic species (Tilman 1997; Naeem 1998). In a review of the literature regarding the diversity-stability debate, Ives and Carpenter (2007) found that 69% of studies reported a positive relationship whereby greater species diversity was associated with increased ecosystem stability defined using resistance, variability and invasibility criterion. The majority of diversity-function relationship studies have explored plant and aquatic communities and so far there have been few studies, relative to the number of plant diversity-function experiments, exploring the relationship between soil biodiversity and ecosystem function (Bardgett 2002).

Hassall et al. (2006), in exploring the frameworks used in ecological investigations, observed some of the variety of methods used within the study of soil biodiversity (microcosm experiments, pot field studies and ecological models). These variably allow for greater control over additional factors whilst reducing the systems to the factors and processes involved. Heemsbergen et al. (2004) used soil microcosms to study the effect of species number and functional dissimilarity on several ecosystem processes: gross nitrate ion productivity, soil respiration, leaf litter mass loss and fragmentation. It was found that species number had only a minimal effect on decomposition processes whereas the mean functional dissimilarity produced a significant positive regression in the analysis of both leaf matter loss and soil respiration. The authors reached the conclusion that these results were due to contrasting functional attributes. This study focussed on elements of the macrofauna: Annelids, Dilopoda and Oniscidea. The number and composition of the species was altered, though microcosms were limited to a total of eight species, a simplification of real ecosystems. This is by no means the only study into this subject, or the only method for exploring the effect of functional diversity on ecosystem function (see Cole et al. 2006; Petchey et al. 2004; Wagg et al. 2014).

Using phylogenetic methods, Maherali and Klironomos (2007) observed an in vitro effect of fungal phylogenetic diversity on ecosystem function whilst investigating the effect of fungal species composition on ecosystem function (i.e. productivity) of *Plantago lanceolata*. In each treatment eight arbuscular mycorrhizal fungal species were added. It was found that, where the species selected were from two different fungal families, plant productivity increased but where the species were phylogenetically under-dispersed, originating from the same family, the resulting plant biomass was not significantly different to that of the non-mycorrhizal controls. However, on the addition of a third

fungal family (still maintaining a total of eight fungal species) no further increase in productivity was observed, indicating some level of functional redundancy. Although this example is from a different system, i.e. a symbiosis as opposed to a decomposer interaction, it illustrates the principal of functional redundancy.

There are several ecosystem processes that have been measured to provide an indication of function including community respiration, productivity, decomposition rates of various substrates, and water or nutrient retention (Naeem et al., 1995), with appropriate methods of indicating faunal contribution offered by Lavelle et al. (2006). To monitor the biological function of soil, microflora soil respiration was chosen as a proxy measure to aid in detection of any decline in biodiversity by ENVASSO (Jones et al., 2008). Other studies comparing the ecosystem function between treatments (habitat, species number/abundance) look at decomposition and nutrient mineralisation rates (Wieder & Lang 1982). Bardgett and Chan (1999) collected evidence supporting the importance of the role played by soil fauna in facilitating nutrient mineralisation (nitrogen and phosphorus) although an array of soil fauna and microbes are responsible for the decomposition of organic matter, with the roles played dependent on size (Cole et al., 2006; Coleman & Wall 2007).

1.7. Factors affecting soil biodiversity

There are many factors that have already been shown to have impacts on soil fauna assemblages. The abundance and diversity of the soil fauna depend on soil properties including: organic matter content, soil texture, compaction, pH and soil management practice (Turbé et al., 2010) and consequently are profoundly affected by human activities (Lavelle 1996).

1.7.1. Soil

Soil properties determine to a great extent the species abundance and diversity of the soil fauna (Cole et al. 2006). Soil pH has been found to affect the numerical abundance of a wide variety of soil taxonomic groups: Bacteria, Nematoda, Fungi and Arthropoda (Mulder et al., 2005). The work of Chauvat et al. (2007) suggests that an increase in soil pH adversely affects abundance and biomass of Collembola, from pH 4.3 to pH 5 in grasslands. Soil fauna species compositions of communities are known to vary with pH as different species have different preferences and tolerances; Collembola, Oribatid mites and Isopoda pH preferences have been developed as a bioindicator system for soil acidity (Van Straalen & Verhoef 1997), and at the genus level a strong relationship between biodiversity and local pH has been found for soil arthropods (Mulder et al. 2005).

Any effect of pH is not purely due to the relative concentration of $[H^+]$ ions, because pH affects nutrient mobility, adsorption and precipitation through the soil (primarily metal ions, thereby affecting phosphate mobility), which in turn can alter soil carbon (C): nitrogen (N): phosphorus (P) ratios. Different species contain different ratios of these nutrients (Wallwork 1976). Soil fauna species with faster growth rates have lower N:P and C:P biochemical ratios. This may make them more susceptible to P based food quality restraints and it has been hypothesised that P availability directly affects the biomass size spectrum of soil fauna groups (Mulder & Elser 2009).

The soils of the RHS Garden Wisley sites, where this study is based, predominantly belong to the Bagshot beds soil formation, characterised by sandy loam which is free draining and of low fertility (Phillips & Armitage 2010) and low pH; pH 5.9-6.3 for the study sites (NRM laboratoies 2009). None of the Collembola indicator species used by Van Straalen

and Verhoef (1997) have a median pH preference within this range; of the eight species chosen three have been recorded at the RHS experimental sites in this study. Two of these are the closest indicator species, falling either side of the observed study site pH (*Orchesella cincta* median pH 5.7, *Lepidocyrtus cyaneus* median pH 6.6) whilst the other is *Parisotoma notabilis* (syn. *Isotoma notabilis*) a notoriously ubiquitous species (Chauvat et al. 2007; Hopkin & Shaw 2013).

Soil pollution affects elements of soil biodiversity, for example Collembola species compositions vary with levels of heavy metal pollution (Fountain & Hopkin 2004). Estimates of species richness and evenness were used to assess the effects of copper, zinc, cadmium and lead pollution on Collembola communities and the most heavily polluted site was found to harbour populations with just a few dominant species with the majority of species being rare. This is a pattern characteristic of communities undergoing stress (Fountain & Hopkin 2004). The presence or absence of metal sensitive species has been suggested as a possible bioindicator system for assessing site pollution to improve on total Collembola abundance as a measure, or species diversity indices, both of which have been found to be unreliable (Fountain 2002; Filser 1995). The population structure of *Folsomia candida*, a common Collembola species used as a 'standard' soil arthropod in laboratory studies (Fountain & Hopkin 2005; Hopkin 2007), was found to have increased mortality and decreased reproductive output in soils retrieved from the most contaminated sites when compared to the other less contaminated sites studied (Fountain & Hopkin 2004). Hågvar and Abrahamsen (1990) also observed differences in collembolan community structure this time for a naturally lead-polluted soil, recognising groups of species sensitive to this environmental factor, but also noting that other species

benefitted: *Isotoma olicacea*. The soil fauna has a range of different levels of sensitivity and tolerance.

1.7.2. Land management

Both soil fauna and consequently the ecosystem processes they support are affected by landscape management. Practices such as tilling, addition of fertilisers or pesticides, compaction and grazing can alter the physical and chemical properties of the soil. Bardgett & Cook (1998) reviewed the effect of a selection of factors associated with land management, including grazing and the application of fertilisers, on several soil fauna groups: nematodes, microarthropods (including Collembola and Acari) and Lumbricidae. Herbivores play an important part in ecosystems as grazing accelerates nutrient incorporation into the soil; both Collembola and Acari numbers at the soil surface were found to decline along a gradient towards reduced grazing in a study of upland grassland (Bardgett, et al. 1993) although other studies mentioned reported reductions with increased stocking densities (King & Hutchinson 1976). In both cases, however, changes in Collembola assemblage structure were noted, showing importance of grazing as a factor. Grazing level is not generally a consideration in gardens as large herbivore contribution to the ecosystem is often removed, although pruning and mowing could be considered equivalent.

Tilling and ploughing are common practices in the management of agroecosystems, they both turn and disturb the soil thus altering its structure. Soil macro-invertebrate communities were found to be both less diverse with lower species abundances in more managed crop systems compared to forests (Nuria et al., 2011). These processes can also result in soil compaction which can reduce the available habitable pore space availability

(Larsen et al. 2004). Insecticides are used to prevent insect damage to crops, so it is unsurprising that their application results in a decline in microarthropod diversity. In grassland communities subject to DDT treatment the collembolan species composition exhibited a different life-history trait distribution i.e. greater abundance of thelytokously reproducing species (Siepel 1996).

Liming is an agricultural and horticultural practice whereby materials rich in calcium or magnesium are added to the soil to raise alkalinity. In an acid grassland, liming was found to increase Collembola abundance, but have no significant effect on the numbers of Acari and both reduced enchytraeid abundance and altered the species composition (Cole et al. 2006). Griffiths and Bardgett (1997) also found that certain components of the mesofauna responded to changes in pH; fewer were found in acid conditions. Chauvat et al., (2007) collected Collembola abundance and diversity data for sites that had been converted from arable land to managed grassland (previously fertilised) detecting the greatest change in the first ten years following cessation of agricultural practices. They noted that the different plant communities arising from succession and grassland management influenced the biomass and composition of the soil fauna as a whole, with differences effecting abundance and biomass, although no significant effect of liming was found specifically for diversity (Chauvat et al. 2007).

1.7.3. Season and climate

The UK has a temperate climate and seasonal fluctuations in soil mesofauna abundances have been well documented with peak abundances generally observed in the autumn (Petersen & Luxton 1982). Usher et al. (1982) found the lowest Collembola abundances during the winter and in general greater numbers of microarthropods are found in the

summer than in winter (King & Hutchinson 1976). For Collembola this has been associated with temperature tolerance; there are fewer Collembola species active between 4 °C and -4 °C (Christiansen 1964). The peak in population size in autumn can be explained by abiotic factors; soil fauna, in particular Collembola, enchytraeids and nematodes are susceptible to low moisture levels which are less frequent in the wetter months (Nielsen 1955; Christiansen 1964). These groups are vulnerable to desiccation and soils that are classified as dry usually containing the lowest densities (Petersen & Luxton 1982) whilst increases in microarthropod abundance at the soil surface are observed following periods of rainfall (Greenslade 1981). When studying soil fauna communities it has been suggested to survey during the spring (April) or early autumn (October) in order that the samples to reflect the mean conditions of the study site (Usher 1970).

Recent studies have placed emphasis on predicting possible responses of soil fauna to climate change. Cole et al. (2002) predicted that for a blanket peat soil site in Cumbria, northern England, future soil warming (caused by a 2.5°C rise in mean monthly air temperature) could result in an increase in Enchytraeid abundance of 43% with a resulting 11% increase in release of dissolved organic carbon. Temperature has previously been shown to affect the numerical abundance of Nematoda (and Fungi), but did not significantly effect that of either soil arthropods or bacteria (Mulder et al. 2005).

1.8. Vegetation origin

In a study of UK garden flora 70% of the plant species grown were found not to be native, this assessment was based on five major UK cities: Cardiff, Edinburgh, Belfast, Leicester and Oxford (Loram et al. 2008). Similar proportions were observed previously by Thompson et al. (2003): one third of the plants in the Sheffield gardens surveyed were

native with the remaining 67% exotic, mostly originating from Europe and Asia. These figures are close to those observed in the planting choices of Owen; over the first 12 years her garden contained an average of 59% exotic species (Owen 1991; Thompson 2006).

Outside of the garden context, urban areas also harbour an increasing number of exotic species. Using data from the Botanical Society of the British Isles (BSBI) monitoring scheme, which seeks to record the distribution and abundances of all plant species that have not been intentionally planted or cultivated, Roy et al. (1999) found that the flora of urban areas had a significantly greater proportion of exotic plant species than nearby rural areas. This result was due to the combined effect of fewer native plant species in towns and cities and greater exotic species richness (Roy et al. 1999). It is currently unknown what impact this incorporation of exotic plants into gardens and public flower beds may be having on either the diversity or the abundance of the native soil invertebrate fauna assemblages.

Native plants are those that originate from a given area, country or land mass. As the UK and Ireland are islands this delimitation is easier than for other countries, UK native plants have been defined as those present prior to the formation of the English Channel or since the ending of the last glaciation period (JNCC 2003). Webb (1985) outlined criteria to consider when determining whether or not a plant is native: fossil evidence, historical evidence, habitat, geographical distribution, frequency of known naturalisation, genetic diversity, reproductive pattern and possible means of introduction, with 'entomological' evidence of insect associations being added later as an additional consideration (proposed by Preston 1986), see Rich and Pryor (2003) for an example of the application of these criteria. Native status was designated to those plant species with

evidence, or without evidence to the contrary, of their presence before the onset of the Neolithic period (UK: 4000 years BCE) or afterwards provided that colonisation was unaided by man (Webb 1985). Usher et al. (2000) further partitions classifications of native status, providing examples of each categorisation, recognising 'shades of nativeness' within the British flora and these are the definitions adhered to by Scottish Natural Heritage (SNH). For a number of species there is still debate as to their status due to the different delimitations followed and the lack of complete evidence (Pearman 2007). For the 'Plants for Bugs' project assessing the impact of vegetation origin on above-ground biodiversity only plant species that were unambiguously native were select for the native treatment (Salisbury et al. 2015).

Vegetation not native to the chosen country, having recently originated or been introduced from elsewhere, is usually termed 'exotic', this includes neophytes (plants introduced after 1500), though archaeophytes (plants introduced prior to 1500) are not always considered alien (Pyšek 1995). Within the literature the label 'exotic' is often used interchangeably with the term 'alien' and less widely with 'introduced', 'non-native' or 'non-indigenous' (Richardson et al. 2000; Pyšek et al. 2004). The 'Plants for Bugs' project has also categorised a group of exotic plants that are closely related, for example coming from a native genus, as 'Near native'. This flora originates from the northern hemisphere but is not native to the UK, although some of the representatives have become naturalised and can be capable of hybridising with the native vegetation (e.g. *Hyacinthoides* × *massartiana* (Rix 2004)).

1.9. Impact of vegetation origin

It is often assumed that native plants are best for native wildlife, with this reflected in planting policies excluding non-native species (Kendle & Forbes 1997). In an exploration of the justifications behind landscape planting decisions Kendle and Rose (2000) compiled a list of five arguments commonly cited as reasons for planting native plants in preference to exotics. Two of these are contradictory; native plants will grow better as they are more adapted to the climate and have greater disease resistance whilst the second raises the issue of the risk of exotics becoming invasive and outcompeting native plant species (see Levine et al. 2003 for mechanisms). A further two relate to biodiversity; the concern for safe-guarding the genetic diversity of native flora and also its ability to support a greater diversity of associated species. The fifth concerns aesthetics and regional appropriateness, the opinion that only those plants naturally found in a given area should be planted there regardless of whether or not there are any physical negative repercussions.

So should we blindly prescribe to the precautionary principle? Kendle and Rose (2000) give the impression that they definitely did not subscribe to native only gardening policies: '*Too often the use of natives is justified with arguments that sound strong but are actually naïve or anecdotal'*. In an advice book for the public regarding wildlife gardening Thompson (2006) explicitly challenges this 'native is best' notion, giving a thorough rebuttal of this native only bias.

This unfavourable media portrayal and perception of vegetation origin importance, could be due to the negative connotations associated with the terms 'exotic' and 'alien' perhaps due to the frequency with which they appear with the term 'invasive'. Invasive species

were identified as the second greatest pressure at sites protected by Scottish Natural Heritage (SNH 2012). There is no doubt that there are documented cases of exotic plants 'escaping' gardens and becoming naturalised, however, there is a difference between a species that has naturalised and one that has progressed to become invasive, in fact the majority of naturalised species fail to achieve this success (Richardson et al. 2000).

One of the species which has, and that is specifically referred to by Roy et al. (1999), is *Buddleja davidii*; commonly called the butterfly bush. This taxon is classified by the BSBI as an alien species and is considered invasive in several countries (e.g. New Zealand (Howell 2008)), however, it also features on many lists of wildlife friendly plants. The English Nature report notes that it is considered to have strong positive environmental impacts (Hill et al. 2005) with both Natural Resources Wales (CCW 2012a; CCW 2012b) and the RHS (RHS 2011) recommending *Buddleja* spp. for encouraging pollinating insects.

The introduction of exotic plant taxa can, however, potentially facilitate the establishment of microarthropod taxa that are associated with them. In an English Nature audit of non-native species (Hill et al. 2005) a table of non-native animal taxa recorded within gardens was compiled, this included two non-native nematodes (*Paratrichodorus renifer* and *Tylenchorhynchus claytoni*) both of which were found on *Rhododendron* spp.. Due to the complex interactions involved it is difficult to predict the effect of species loss or the introduction of any new taxa to systems on ecosystem functions, though Heemsbergen et al. (2004) show that functional dissimilarity may play a key role.

De Deyn et al. (2004) found that both plant species and plant diversity affected the diversity of soil nematodes. The study consisted of comparisons of the nematode

diversity found in monocultures to that obtained from plots planted with different combinations of eight plant species. In 2010 Orwin et al. explored the effect of a selection of plant traits on the functioning of a temperate grassland ecosystem. The plant species with a high relative growth, that tended to have leaves and litter with greater nitrogen concentrations, were associated with increased bacterial biomass levels (relative to fungi) and greater rates of mineralisation (Orwin et al. 2010), however, this study did not record any data for soil mesofauna. Chauvat et al. (2007), in a study focusing on the effect of land use change on Collembola communities, found that total Collembola abundance (combined epedaphic, hemiedaphic and euedaphic) was positively related to both plant diversity and vegetation cover. This study will extend that of Chauvat by looking at the effects of a wider variety of flora, with a greater range of origin, on a larger sector of soil biodiversity whilst also exploring the effect on ecosystem processes.

Plants influence soil properties through their roots, this region is termed the rhizosphere and its impact decreases with increasing distance creating biological and physiochemical gradients. These influences extend from the root surface and can be lengthened by interactions with fungi: mycorrhizosphere (Lavelle 1996). Possible mechanisms for exotic species affecting soil biodiversity include the alteration of soil properties, through interactions in the soil rhizo/mycorrhizosphere (Levine et al. 2003). Exotic plants could also have differing nutrient requirements.

Other possible mechanisms involve alteration of habitat structural properties. Vegetation cover has previously been reported to influence the distribution of microarthropod groups. House et al. (1987) suggested that a decrease in the vegetation canopy and the cover it provides alters the microclimate available to microarthropods by affecting

temperature and soil moisture content. Shaw and Usher (1996) found that, of the thirteen most commonly found Collembola species at a plantation (coniferous woodland), twelve were correlated with the distribution of vegetative cover. Certain exotic species may also be less resilient to the UK climate or have different vernalisation requirements which could result in altered provision of cover. The foliage of plants with a different vegetation origin may emerge, senesce and abscise at different seasonal points to native flora which could also potentially result in altered provision of cover as well as litter availability. Exotic plants could also have differing leaf litter nutrient properties (biomass, secondary metabolites); as availability of plant material is also related to the abundance of soil fauna this could also affect community structures (Bardgett & Cook 1998).

Smith et al. (2006) looked at the predictors of invertebrate species richness in urban domestic gardens. They found that the abundance of trees and other components of garden vegetation were important factors, however, observed patterns were not consistent across all the taxa studied and the soil fauna were neglected (it is worth noting that leaf miners were one of the groups studied so perhaps unsurprising that their presence was correlated with tree number). At a larger scale Kennedy and Southwood (1984) investigated the association between invertebrate assemblages and British trees across the UK confirming previous work in identifying host tree abundance as the best factor for accounting for differences in species richness. The more abundant trees (e.g. *Crataegus monogyna* (Hawthorn)) were associated with a greater number of insect species.

Kennedy and Southwood (1984) also explored the factor of time of residency within Britain, suggesting that the number of years a tree had been present has a role in

predicting the number of insect species it supports. This implies that the more recently the vegetation has arrived (exotic species); the fewer accumulated insect associations and species benefitting from its presence, supporting a 'plant native' view point. An example would be that of *Acer pseudoplatanus* (Sycamore) which is a non-native naturalised species (Townsend 2008). Kennedy and Southwood (1984) recorded abundance of 48,311 Sycamore trees yet only 43 associated insect species in contrast to the two *Quercus* spp. (Oaks) which, when combined, had a similar abundance (49,707 trees) but had 423 associated insects. Kennedy and Southwood used establishment dates of 650 years and 9000 years for Sycamore and the Oaks, respectively. However, this does not necessarily mean that the non-native Sycamore is of no conservation benefit; opinions as to its value differ (Bingelli 1993). Townsend (2008) does list several ponts in its defense, one of the main ones being that there have been records of Sycamore providing a habitat for red data book species (Whitehead 2005), however, of the four listed species found one has now been removed. *Cicones undatus* (a Coleoptera) had been found on Sycamore and was previously a red data book species (Whitehead 2005), but has now been taken off the list as evidence suggests that it is a natuarlised species (Natural England 2014b). The topic of soil biodiversity, underneath native vs exotic planting, was not explored by Kennedy and Southwood (1984), however, Shaw and Usher (1996) found that levels of Collembola species richness under a monoculture of the non-native *Pinus contorta* (Lodgepole pine) were comparable to those encountered in native UK ecosystems.

An updated phylogenetic approach was undertaken by Kelly and Southwood (1999), incorporating phylogenetic relationships via independent contrasts (Felsenstein 1985). They again found that host tree availability was the greatest predictor, however, when only native trees were analysed this had a reduced predictive value. One of the reasons

proposed by the authors is that native and non-native trees have different proportions of generalist and specialist herbivores: native trees having accumulated more specialist species than introduced trees. It is not currently known whether this extends to the soil biodiversity beneath or to shrubs and herbaceous plants found within gardens with their range of vegetation origins and differing introduction times.

In the context of urban domestic gardens the number of alien or native plant species present was only important in a 'tree' analyses where models were used to check that the robustness of inferences from multiple regression, where data was partitioned with respect to the independent variables measured (Smith et al. 2006). In a subsequent analysis of data collected from the same set of gardens a strong positive relationship between native plant richness and the abundance of hoverflies and solitary bees was shown (Smith, et al. 2006). Here both the richness of native and exotic higher plant taxa and their proportions were included as independent variables with plant nativity status following Stace (1997). The hoverflies and solitary bees were only two of the twenty-two invertebrate groups selected for study, however, soil cores were not taken so any effect on soil biodiversity could not be assessed. Although Collembola would have undoubtedly been recovered in the litter samples collected though they were not identified or analysed.

1.9.1. RHS 'Plants for Bugs' project

In order to investigate the question of the effect of plant origin on biodiversity, the Royal Horticultural Society (RHS) set up experimental plots, located at the RHS Wisley Garden in Surrey, colloquially called the 'Plants for Bugs' project (P4B) (RHS 2009). A randomised split-plot experimental design was employed, see Perry et al. (2003) and Squire et al.

(2003) for the philosophy behind this type of experimental plot layout. The project has two study sites, Deer's Farm and Howard's Field, which were planted with flora originating from three different geographic area treatments: UK Native, Near native; from the northern hemisphere, and Exotic; from the southern hemisphere, see Salisbury et al. (2015).

Within each vegetation origin treatment there were three plant species groups, e.g. Native plant group A, B and C. Thompson (2006) points out that UK wildlife is usually present in the rest of Northern Europe in habitats with plants that would be considered exotic if found growing here, soil biodiversity is not explicitly mentioned, however, it is a logical extension of this line of reasoning and so it is here that the Near native category could help to tease out any differences between exotic flora that has been separated from the UK fauna for a long period of time to that where there is still overlap.

The 'Plants for Bugs' project focussed on the above ground invertebrate fauna and was a natural experimental extension of the BUGS surveys. This research tested the popular assumption that native vegetation species are best for encouraging invertebrate biodiversity, using a variety of sampling methods: (e.g. pitfall-traps, vortis sampling and direct observations of insect flying visitors) to assess and compare the abundance and diversity, whilst collecting an array of co-variate data to explain any differences observed. The work presented here analyses the soil fauna of the 'Plants for Bugs' project.

1.10. Summary

The overarching aim of this project was to discover whether the geographical origin of vegetation affected soil faunal assemblages and decomposition rates for a UK soil. To achieve this, the objectives were as follows:

- To describe the study sites and their soil properties; to determine any differences between the soil properties of the plots planted with the differing vegetation origin treatments (Chapter 2.).
- To collect soil samples from the RHS experimental plots, then extract and identify the soil fauna in order to characterise the soil biodiversity (taxonomic) (Chapter 3.).
- To calculate metrics of soil fauna community composition (Collembola) and compare them between the Native, Near native and Exotic vegetation origin treatments (Chapter 3.).
- To collect a DNA sequence from each Collembola species present, for one sampling occasion, in order to characterise the soil biodiversity (phylogenetic) of the RHS experimental plots (Chapter 4.).
- To calculate metrics of soil fauna phylogenetic diversity and compare them between the Native, Near native and Exotic treatments (Chapter 4.).
- To use litter bags to obtain decomposition rate data (Chapter 5.).
- To analyse any differences in decomposition rate data between the Native, Near native and Exotic treatments (Chapter 5.).

The study presented here complements the aims of the 'Plants for Bugs' research conducted by the RHS, and was the only component of the project to look outside the

plots; it also compared the soil fauna communities of the garden sites to that of less intensively managed habitats. Samples were collected from the amenity grassland sites adjacent to the experimental plots, to provide a background level of species diversity, whilst the nearby semi-natural woodland; Buxton Wood and the lowland heath of Wisley Common were selected for comparison.

Traditional extraction and identification methods followed by both the calculation of diversity indices and a molecular phylogenetic approach were used to analyse the soil fauna communities. Decomposition rates were assessed for each plot, using both twig and leaf litter bags for the soil mesofauna and bait lamina strips for earthworm activity. The implications of all results have been discussed with regards to the management of gardens for biodiversity.

Chapter 2. Site descriptions

2.1. Introduction

2.1.1. Site locations

There are four study sites: Deer's Farm and Howard's Field which are both located within the Royal Horticultural Society (RHS) Gardens Wisley, Wisley Common and Buxton Wood. All sites are situated in the north of the county of Surrey, south-west of London, close to the village of Wisley. All sites are located within a circle with a radius of 560 m centred on TQ 06837 59144, see Figure 2.1.1..

Figure 2.1.1. Map of the study area overlaid with a OSGB 100 m grid, labelled with the locations of the study sites adapted from Chadwick (2014).

The Deer's Farm and Howard's Field sites consist of the RHS experimental plots and adjacent grassland plots 4 m to the south and 2 m to the north respectively. Howard's Field is situated within the main grounds of the RHS Gardens at Wisley and Deer's Farm is situated 150 m to the north-east of this. Buxton Wood is 850 m north-east of Howard's Field and Wisley Common is 800 m south-east of Howard's Field. Buxton Wood and Wisley Common are the furthest apart (~1050 m).

2.1.2. Site geology

All study sites are on the Bagshot Beds formation, which is characterised by acid sandy loam soils which are free draining and of low fertility (Jarvis et al. 1984; Phillips & Armitage 2010). Figure 2.1.2. shows a map of the study area showing the known boundaries between the Bagshot Beds and London Clay formations.

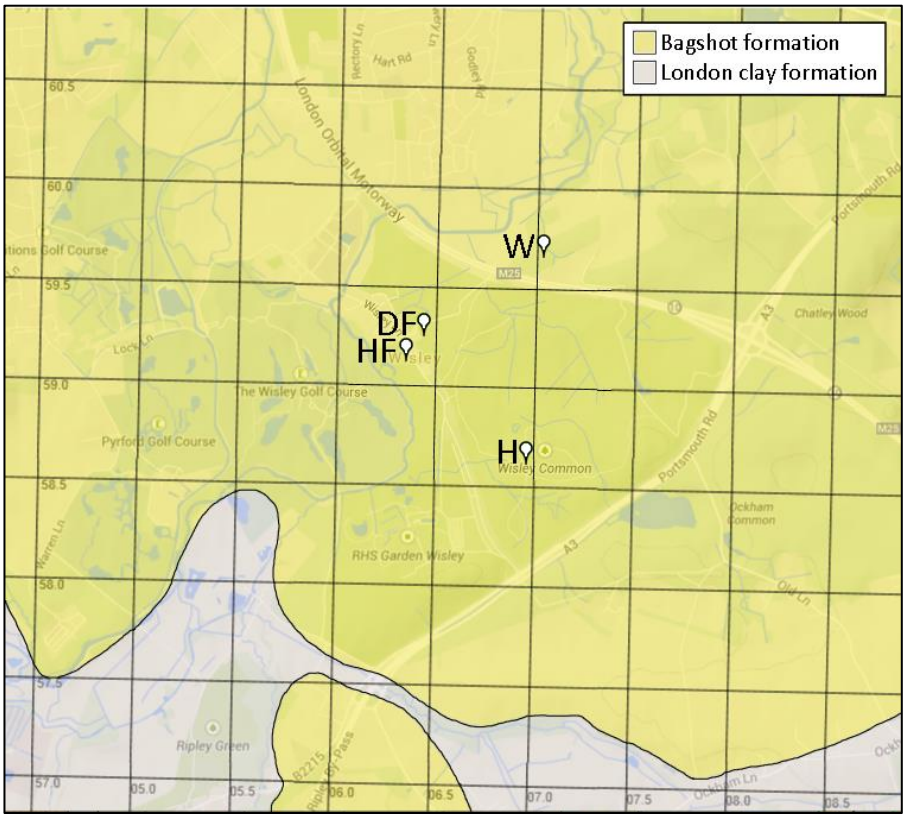

Figure 2.1.2. The study area overlaid with bedrock mapping information from the British Geological Survey, adapted from Chadwick (2014). Study sites are labelled: HF: Howard's Field, DF: Deer's Farm, W: Buxton Wood and H: Wisley Common.

This soil bed dates back to the formation of the Hampshire and London basins in the upper Eocene, Tertiary era, whereby the fine sandy deposits of the Bagshot Beds succeed the London Clays (Jarvis et al. 1984). Overlaying this are superficial deposits; the Deer's Farm, Howard's Field and Buxton Wood sites are situated over Kempton Park Gravel deposits, see Figure 2.1.3., however, the superficial deposits have not been previously recorded for the Wisley Common site. The soils of the sites are part of the Swanwick association which are coarse loamy and sandy soils that can be affected by fluctuating groundwater levels in sandy and loamy drift containing flints (Jarvis et al. 1984; Cranfield University 2014a).

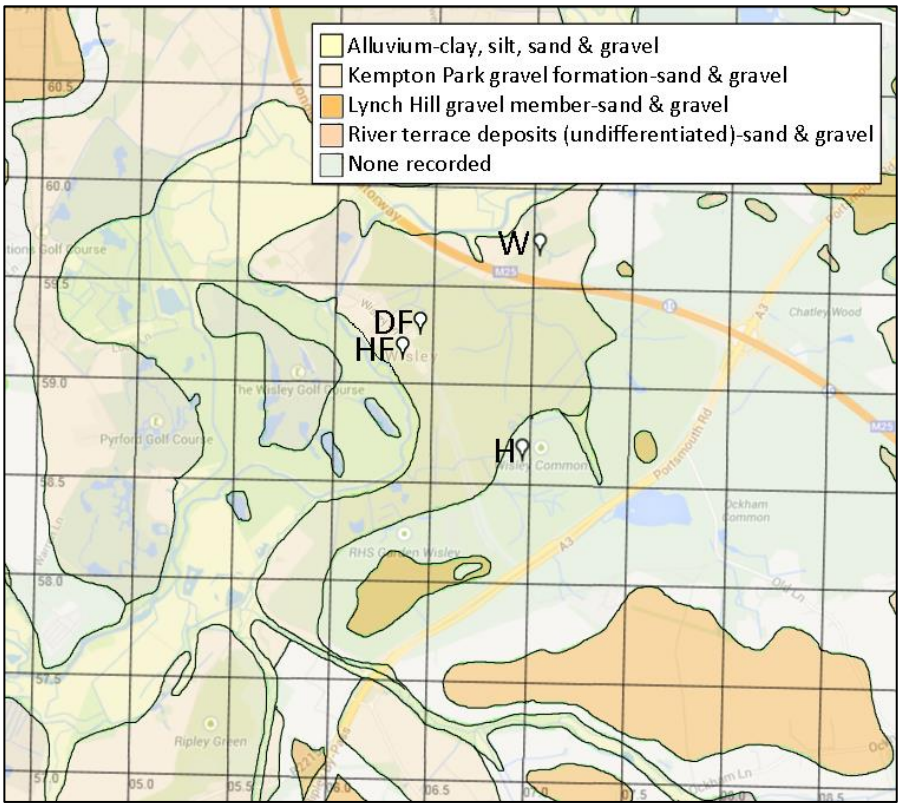

Figure 2.1.3. The study area overlaid with superficial deposits mapping from the British Geological Survey, adapted from Chadwick (2014). Study sites are labelled HF: Howard's Field, DF: Deer's Farm, W: Buxton Wood and H: Wisley Common.

2.1.3. Site descriptions: RHS experimental plots and adjacent sites

The garden at Wisley was founded as a horticultural garden in 1878 before becoming an RHS garden in 1904; the areas containing the two RHS study sites at Howard's Field (TQ 063 591) and Deer's Farm (TQ 064 592) were added in 1903 and just after WWI

respectively (Phillips & Armitage 2010), with the vegetation for the 'Plants for Bugs' project being planted between May 2009 and June 2010 (Salisbury et al., 2015). Over the years of management, additional nutrients have been added to improve the soil for horticultural purposes which have raised the pH across the garden (Phillips & Armitage 2010), however, no fertilisers have been added to the experimental plots since the application of magnesium sulphate at 60 g/m^2 and sulphate of ammonia at 16 g/m^3 in July 2009 at the Deer's Farm site only (Salisbury et al., 2015). A soil analysis, carried out in April 2009, measured the pH of the two RHS experimental plot sites: Deer's Farm had a pH of 6.3; whilst Howard's Field was more acidic at pH 5.9. The Deer's Farm site is more exposed than that of Howard's Field which is situated within the main garden at RHS Wisley and is sheltered on three sides by trees which serve as a wind break.

In addition to the established RHS experimental plots the adjacent grassland of both the two sites was also sampled. These areas have essentially been managed as amenity grassland or lawns and have not had additional fertilisers applied. In May 2012 species lists were made of both the Deer's Farm and the Howard's Field adjacent sites: vascular plant species present are listed alphabetically by family in Table 1. and the non-vascular plant species are listed in Table 2. (Appendix 2.1.).

Both the adjacent grassland soils are very sandy with shallow rooting zones. In the Deer's Farm adjacent site profile there was no O horizon (organic matter) and the A horizon (topsoil/mineral horizon), a dark loamy sand, extended down to a depth of 22 cm within which a few flints were retrieved from the lower layers, below this was a pale brown sandy C horizon, see the soil profile photo in Figure 2.1.3a. For the Howard's Field site,

the soil profile photo taken in Figure 2.1.3b., no O horizon can be seen and the A horizon is also a loamy sand which extends down to at least 20 cm.

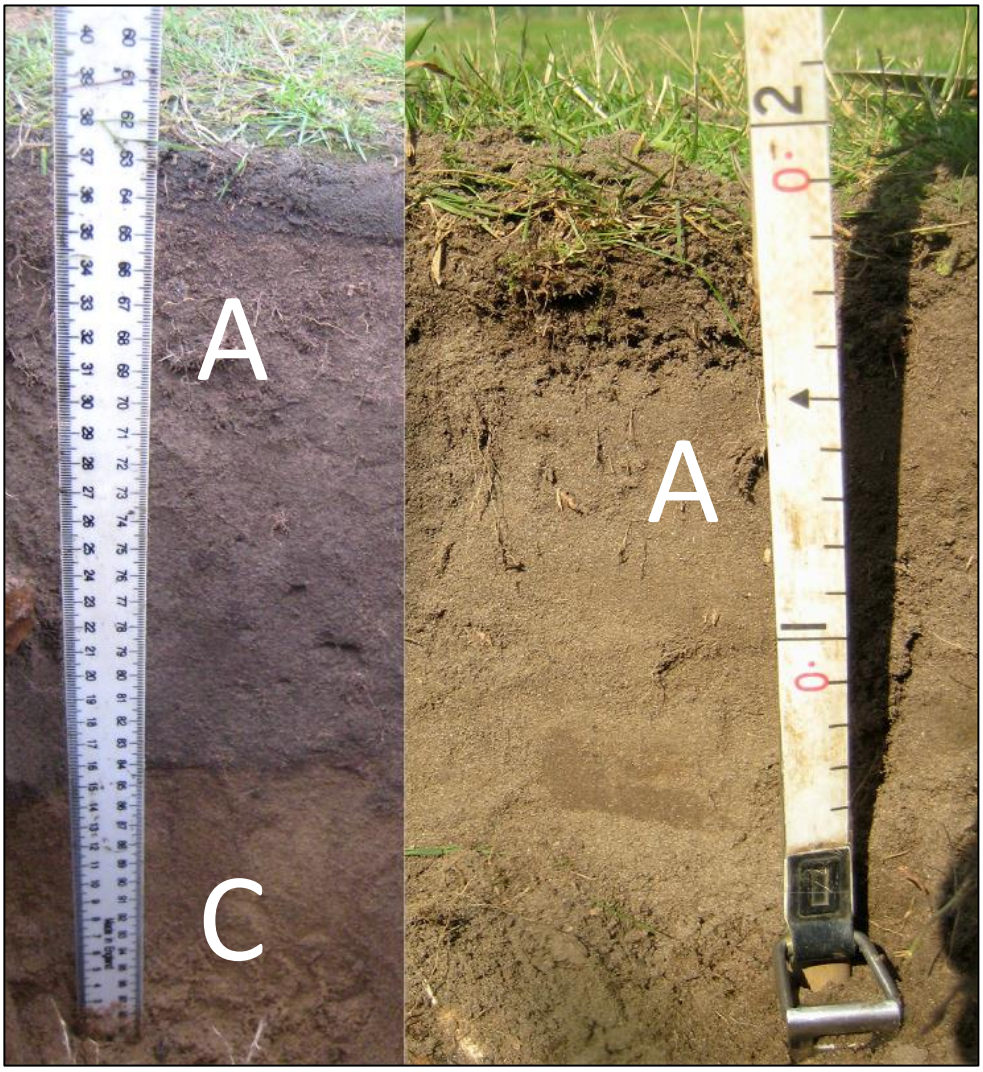

Figure 2.1.3a. (Left) Soil profile of the grassland site adjacent to the RHS experimental plots at Deer's Farm to a depth of 55 cm (the darkening of the top 2 cm was due to heavy rainfall), scale in cm. **Figure 2.1.3b.** (Right) Soil profile of the grassland site adjacent to the RHS experimental plots at Howard's Field, scale in cm.

2.1.4. Site description: Wisley Common

Wisley Common is a heathland situated to the south-east of Deer's Farm. Heaths are semi-natural habitats characterised by nutrient poor acidic soils where members of the Ericaceae (heather family) are generally among the dominant species (Rodwell 1991). These heathland plagioclimax communities were created by deforestation and subsequent deterioration of the soil due to agricultural (intense cultivation) or pastoral practises commencing in the neolithic period: where the soil became too acid the sites

were left to become heaths, which were then maintained by animal grazing (Dimbleby 1984). Evidence of Bronze Age occupation has been found at Cockcrow Hill on Wisley Common and from 1086 there are records of the land being part of the manorial commons of a manor at Wisley (Currie 1997). There are records of the land being used to graze animals and as this practice declined, woodland species encroached on the heathland, until from an aerial survey in 1988 little remaining heathland was observed. A thorough evaluation of the historic landscape of Wisley Common has been undertaken by Currie (1997).

Wisley Common is now a site of special scientific interest (SSSI): it is a lowland heath within which is Unit 5 a 62 hectare area of dry dwarf shrub heath (TQ 069 587) (Natural England 2014a). The condition of this area was last assessed in September 2011 and was described as favourable (Steven 2011), the site prescribed by Surrey Wildlife Trust for sampling is situated at TQ 0695 5872 within this Unit. Species lists made in May 2012 of vascular plants can be found in Table 3. and of bryophytes and lichens in Table 4. (Appendix 2.1.). The study site is dominated by *Calluna vulgaris* (L.) Hull (ling), with occasional *Betula pendula* Roth (silver birch) saplings and *Molinia caerulea* (L.) Moench (purple moor grass). The soil surface is covered by a mix of bryophyte and lichen species as well as young *C. vulgaris* plants. Since 2007 the site has been grazed in the summer by cattle (Belted Galloways) with the aim of preventing invasion and succession by woodland species: *B. pendula*, *Pteridium aquilinum* (bracken) and *Pinus sylvestris* L. (Scots pine).

The soils of Wisley Common site belong to the Swanwick association, Isleham soil series (Cranfield University 2014a; Cranfield University 2014c). Lackenheath soils have also been found at Wisley Common although these were identified under the wet heathland

areas (Jarvis et al. 1984; Cranfield University 2014b), the study site was situated on a raised bank so it is not subjected to the seasonal waterlogging. The O horizon of the heathland soil profile extends down 4-6 cm followed by an A horizon at 6-43 cm which is lightly mottled in the lower regions, below this is an E (eluvial) zone, see soil profile pictures Figures 2.1.4a. and 2.1.4b..

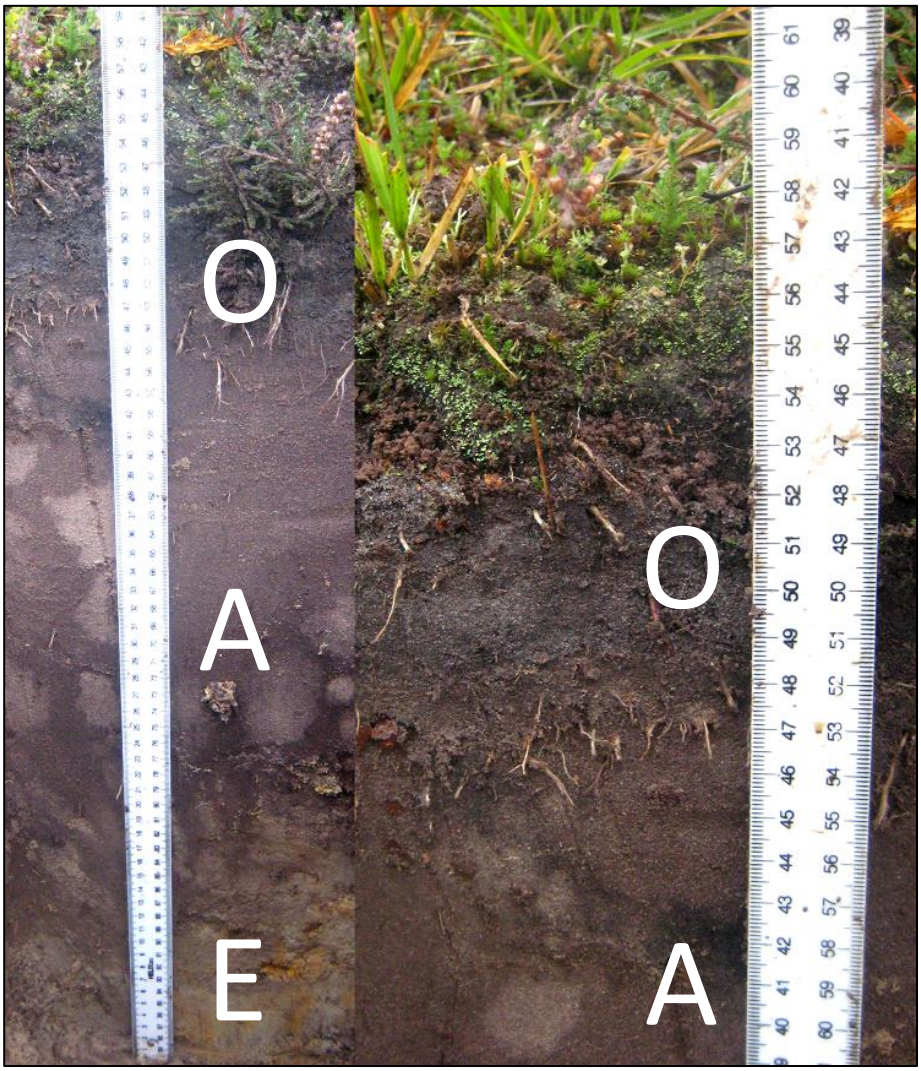

Figure 2.1.4a. (Left) Soil profile of Wisley Common to a depth of 55 cm. **Figure 2.1.4b.** (Right) Soil profile of Wisley Common: close up of the top 15 cm of the soil profile. Both scales in cm.

2.1.5. Site description: Buxton Wood

Buxton Wood is a broad-leaved semi-natural woodland (TQ 070 596), see species lists, made in May 2012, of vascular plants in Table 5. and bryophytes in Table 6. (Appendix 2.1.). The site is dominated by *B. pendula* with frequent *Quercus robur* L. (English oak) and occasional *Fagus sylvatica* L. (beech).

Across the study site there is a litter layer comprised mainly *of Q. robur* leaf material 2-6 cm thick. Figures 2.1.5a. and 2.5.1b. show two soil profiles taken from Buxton Wood. In Figure 2.5.1b., taken from the middle of the study site, there is a clear O horizon 8 cm thick below which is the A horizon, which then gives way to a C horizon at a depth of 40 cm. The profile in Figure 2.1.5b., taken from immediately adjacent to the study site, has a thinner O horizon (~3 cm) and looks to be a buried profile probably the result of animal disturbance: rabbits, foxes and badgers are present in the area. It has a C horizon approximately 6 cm thick followed by an A horizon and a second C horizon starting at a depth of 38 cm.

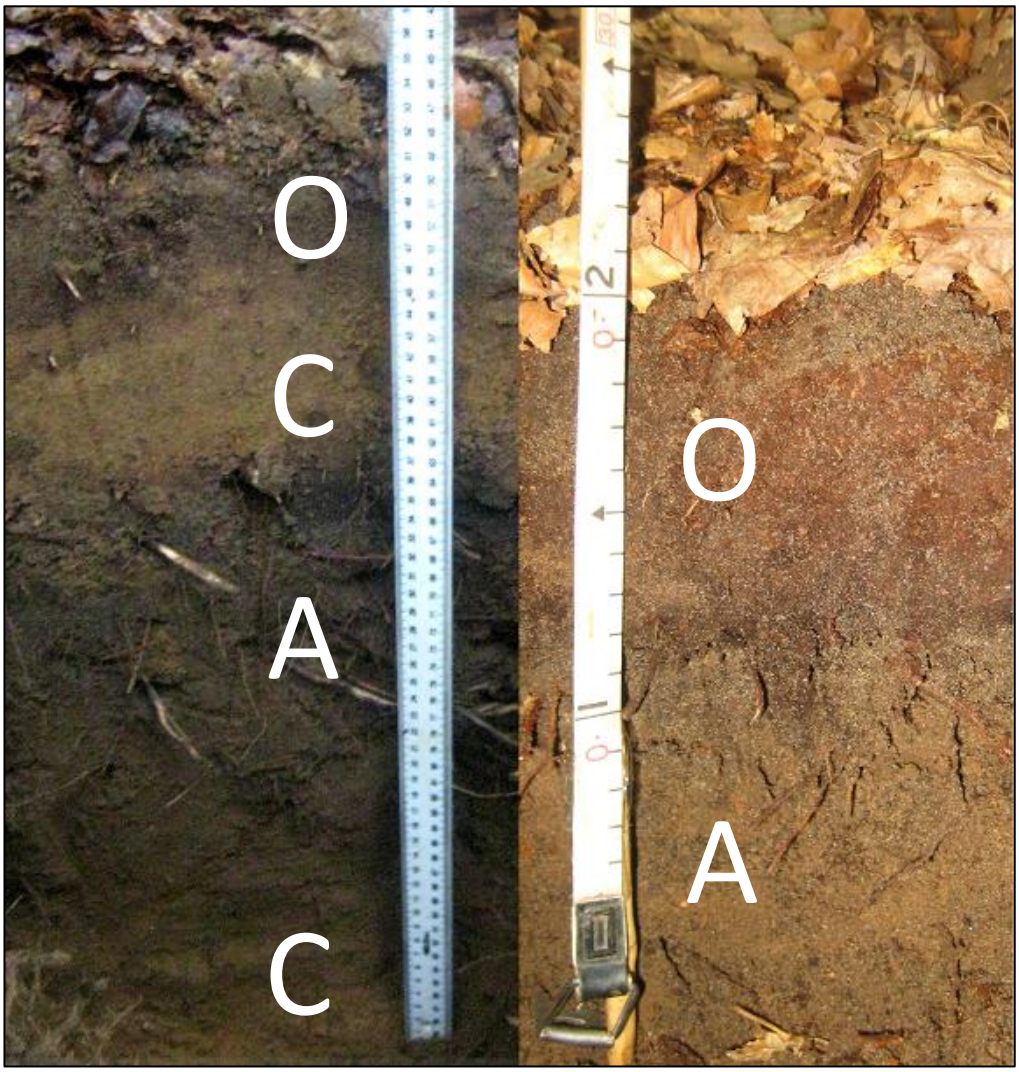

Figure 2.1.5a. (Left) Soil profile of Buxton Wood to a depth of 55 cm. **Figure 2.1.5b.** (Right): Soil profile of Buxton Wood: top 20 cm taken from a secondary location showing a deeper layer of organic material (O horizon). Both scales in cm.

2.2. Methods

2.2.1. Experimental design

The RHS experimental plots, established in 2009, follow a randomised split-plot design; at both of the two field sites (Deer's Farm (18 plots) and Howard's Field (18 plots)), each site was split into six blocks running from top to bottom in two halves as you look at Figure 1. and Figure 2. Appendix 2.2.. Within each of the blocks the three vegetation origin treatments were then randomly assigned such that each block contained one Native plot, one Near native plot and one Exotic plot. The species selected for the Native treatment were unambiguously native, the Near native plants naturally occur in the northern hemisphere, but are not present in Britain and the Exotic species originate from the southern hemisphere (Salisbury et al., 2015).

Within each planting treatment there were three different plant species groups, i.e. Native plant group A, B and C, Near native plant group A, B and C, Exotic plant group A, B and C. These three planting mix groups ('A', 'B' and 'C') were assigned to the 6 blocks (so at each site there were two blocks 'A', two blocks 'B' and two blocks 'C') using restricted randomisation to ensure an even distribution (from left to right as you look at Figure 1. and Figure 2. Appendix 2.2.). See Appendix 2.2., Table 1., for the species used and Salisbury et al. (2015) for plot management protocols and vegetation structure/layout of individual plants within the plots.

2.2.2. Soil co-variate data collection

A research assistant, Michael Terrington, was employed to conduct pH testing on the soils retained from the sample collection. After soil fauna extraction the soil was dried out in an oven at 105 °C for 48 hours, then temporarily stored at room temperature until the

end of each sampling occasion before being transferred to the freezers at the University of Roehampton for long term storage (-20 °C). The pH protocol followed was adapted from Grimshaw (1989). For each sample 5 g of soil was weighed into a universal container. 50 ml of deionised water was then added and shaken for 2 minutes and allowed to settle for 10 minutes. The electrodes of a microcomputer pH meter (make: Hanna, model: HI 9024) were then immersed in the supernatant liquid and the pH recorded when the reading had stabilised.

Further soil analysis (pH; estimation of organic matter content by loss on ignition (LOI); availability of the macronutrients: nitrogen (total available nitrogen (Kg/ha), nitrate: $NO3^-$ (mg/Kg) and ammonium: $NH4^+$ (mg/Kg)), magnesium (mg/l), potassium (mg/l) and phosphorus (mg/l), which are required for healthy plant growth) was outsourced to NRM laboratories (Bracknell) using samples collected specifically for this purpose in September 2014. For each sample, 500 g of topsoil was collected from a randomly selected co-ordinate within each plot to obtain the freshest analyses possible on undried soils samples, they were immediately transferred to labelled bags inside a cool box and sent by courier to the NRM laboratories at Bracknell, where the analytical methods employed are detailed in MAFF (1986).

2.3. Analysis

All statistical analysis was conducted in RStudio (RStudio, 2014), versions “Toasted Marshmallow” and “Spring Dance”. Although ANOVA (analysis of variance) is robust to moderate deviations in normality of data distributions and is sometimes the better choice when sample sizes are small (Khan & Rayner 2003) as here first only the sites (Deer’s Farm, Deer’s Farm adjacent, Howard’s Field, Howard’s Field adjacent, Wisley Common

and Buxton Wood) are being described/compared and the 'treatment' (vegetation origin: Native, Near native, Exotic) is not being considered, this results in an unbalanced statistical design. So, the non-parametric equivalent Kruskal-Wallis was used with the null hypothesis (H0): all samples belong to the same population and the alternative hypothesis (Ha): at least one of the samples does not belong to the same population. Where H0 was rejected the R package "dunn.test" (Dinno 2014) was used to run the Dunn post-hoc tests with a Bonferroni correction: reports the results of the multiple comparisons. An alternative: pairwise comparisons using Tukey and Kramer (after Nemenyi) using the R package "PMCMR" (Pohlert 2014), yielded the same results. These tests are equivalent to the Wilcoxon-Mann-Whitney tests (with Bonferroni correction) but instead use the same ranks as the Kruskal-Wallis test, only the Dunn Q statistics are reported in Section 2.4. as that is the more powerful test (Zar 2010).

There should be no differences in soil properties (pH, macronutrients) between the different vegetation origin treatments within the Deer's Farm and Howard's Field sites, as the experimental plot layout follows a split-plot design with adjacent treatments at 1 m separations (see Appendix 2.2., Figures 1. and 2.), however, the plants came with soil from nurseries and were not grown from seedlings in situ. To check this assumption two-way ANOVAs were performed in R, on just the RHS experimental plot data, with the null hypothesis (H0): all samples belong to the same population and the alternative hypothesis (Ha): at least one of the samples does not belong to the same population, with site and treatment as factors. ANOVA is robust to moderate deviations in normality (here one dataset did not fit the normal distribution, for pH; Shapiro-Wilk: $p < 0.05$) and it is suggested that it is more suitable than the alternatives when dealing with small sample

sizes (Khan & Rayner 2003). The post-hoc Tukey's honest significant difference (HSD) test was performed to explore instances where for an ANOVA factor $p < 0.05$.

A canonical correspondence analysis (CCA) was also performed in RStudio using the R package "vegan" (Oksanen et al. 2014) to visualise how the sites are related based on a set of the soil property parameters measured (pH, available magnesium, available phosphorus, available potassium, LOI and total available nitrogen). A permutation test was performed to determine whether site was a significant factor in the ordination (999 permutations).

2.4. Results

The pH values obtained from the soil samples the fauna were extracted from can be found in Table 1. Appendix 2.4. and the results from the 2014 soil analysis can be found in Table 2., Appendix 2.4.. Overall significant differences were found across different sets of sites in terms of all the soil property parameters measured, see Table 2.4. at the end of this section.

A CCA testing whether the soil properties differed between sites found that site was a significant factor (permutation test: $F_{5, 54} = 13.629$, $p = 0.001$) see Figure 2.4. for a graphical representation.

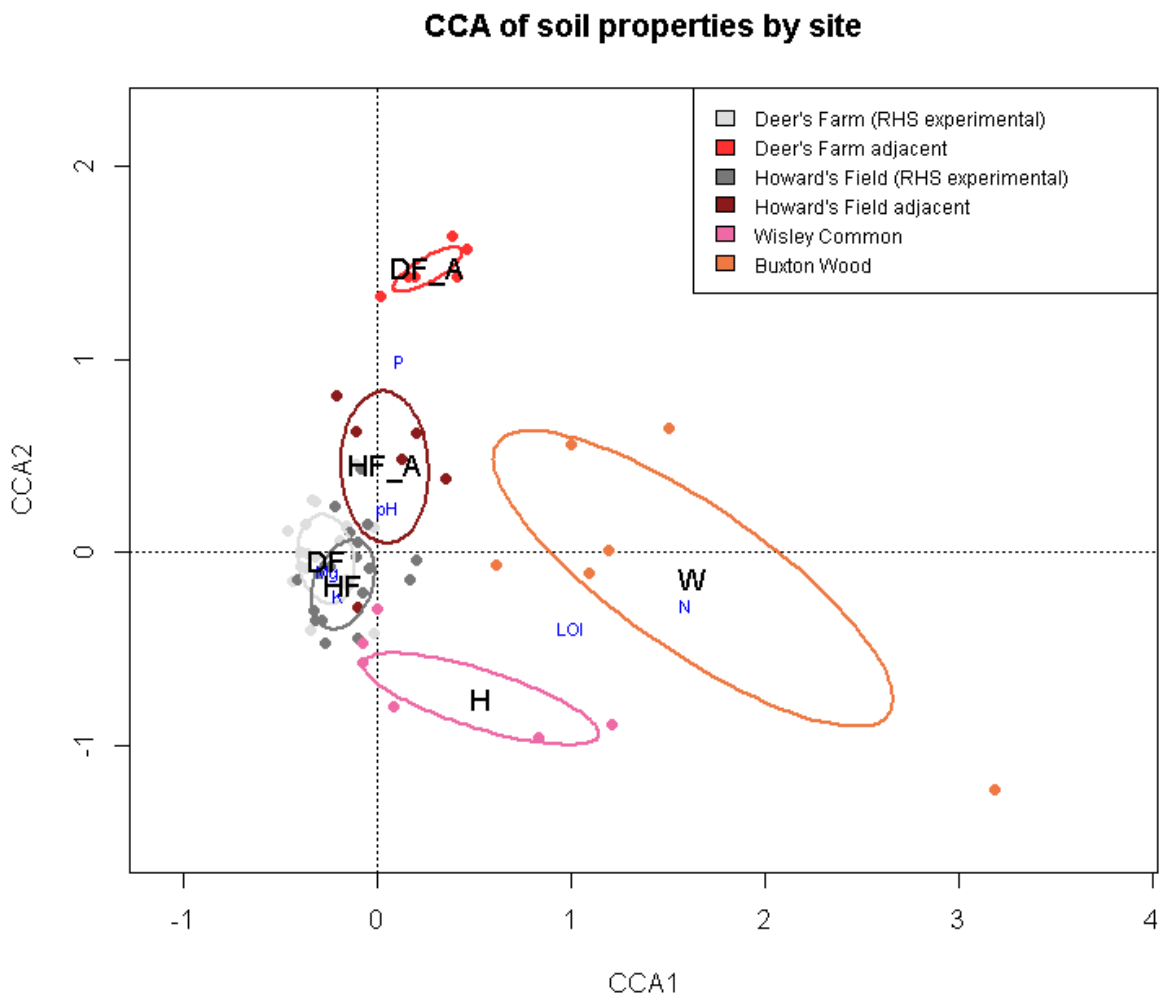

Figure 2.4. CCA ordination diagram of plot soil properties with plots separated by site. Black labels represent site centroids: DF: Deer's Farm, HF: Howard's Field, DF_A: Deer's Farm adjacent, HF_A: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood), from the 2014 NRM soil analysis. Ellipses are plotted using standard deviation from the centroids. Soil property parameters are labelled in blue, from left to right: magnesium (Mg), potassium (K), pH, phosphorus (P), loss on ignition (LOI) and total available nitrogen (N).

2.4.1. pH

A Kruskal-Wallis test revealed a significant difference in pH (NRM laboratories pH values: Table 2., Appendix 2.4.) across all of the sites ($\chi^2 = 53.3$, 5 d.f., $p < 0.001$), H0 was rejected. A post-hoc Dunn test showed where the significant differences between sites lay, see Figure 2.4.1a. for a graphical representation; the sites with the same letter above them do not differ significantly from each other $p < 0.05$, see Table 3., Appendix 2.4. for the full statistical output.

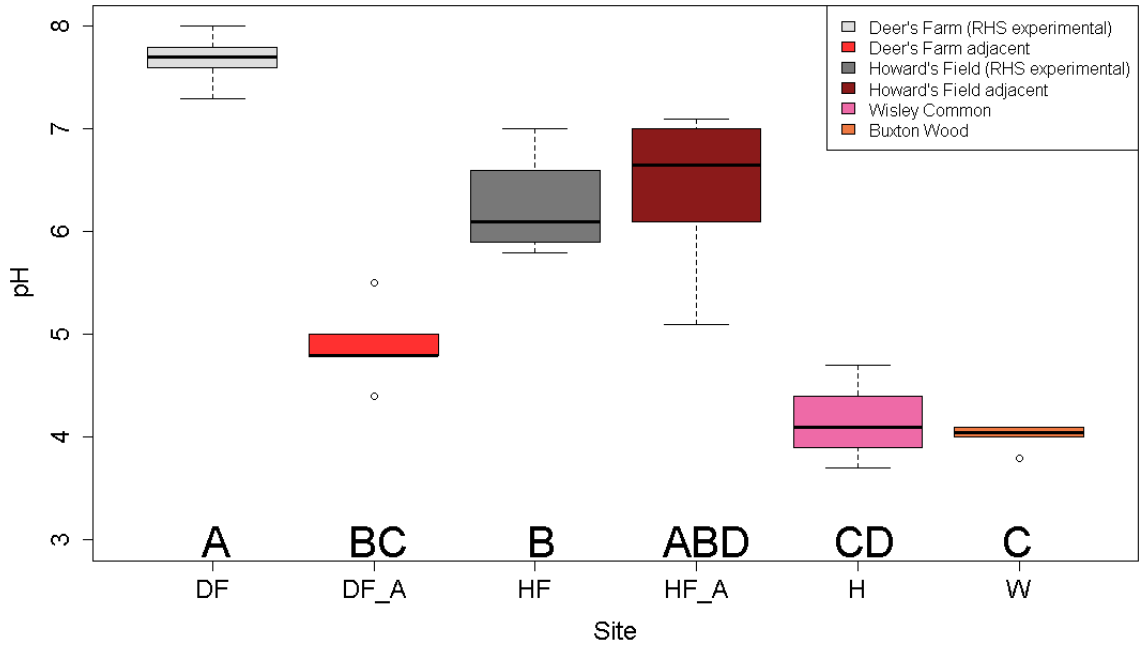

Figure 2.4.1a. Boxplots of pH at each of the sites (DF: Deer's Farm, HF: Howard's Field, DF_A: Deer's Farm adjacent, HF_A: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood), from the 2014 NRM soil analysis. Sites followed by the same letter do not differ according to the Dunn's post-hoc test.

The analysis conducted by NRM laboratories in September 2014 yielded less acidic pHs, than the analysis conducted in 2009. Soil samples taken from each of the RHS experimental plots at Deer's Farm were alkaline, ranging from pH 7.3 to pH 8.0 (mean pH 7.7) and those at Howard's Field were more acidic: pH 5.8 – pH 7.0 (mean pH 6.2), see Figure 2.4.1b. for boxplots where the data has been separated by the vegetation origin treatment.

The site adjacent to the Deer's Farm plots was more acidic pH 4.4 – pH 5.0 (mean pH 4.9) than the RHS experimental plots; though the Howard's Field adjacent site was more similar to that of the experimental plots pH 5.1 – pH 7.1 (mean pH 6.4) (NRM analysis: Table 2., Appendix 2.4.). The soil of Wisley Common is very strongly acidic with a pH ranging between pH 3.7 and pH 4.7 (mean pH 4.2) and the soils of Buxton Wood were also strongly acidic, pH 3.8 to pH 4.1 (mean pH 4.0) (Table 2., Appendix 2.4.).

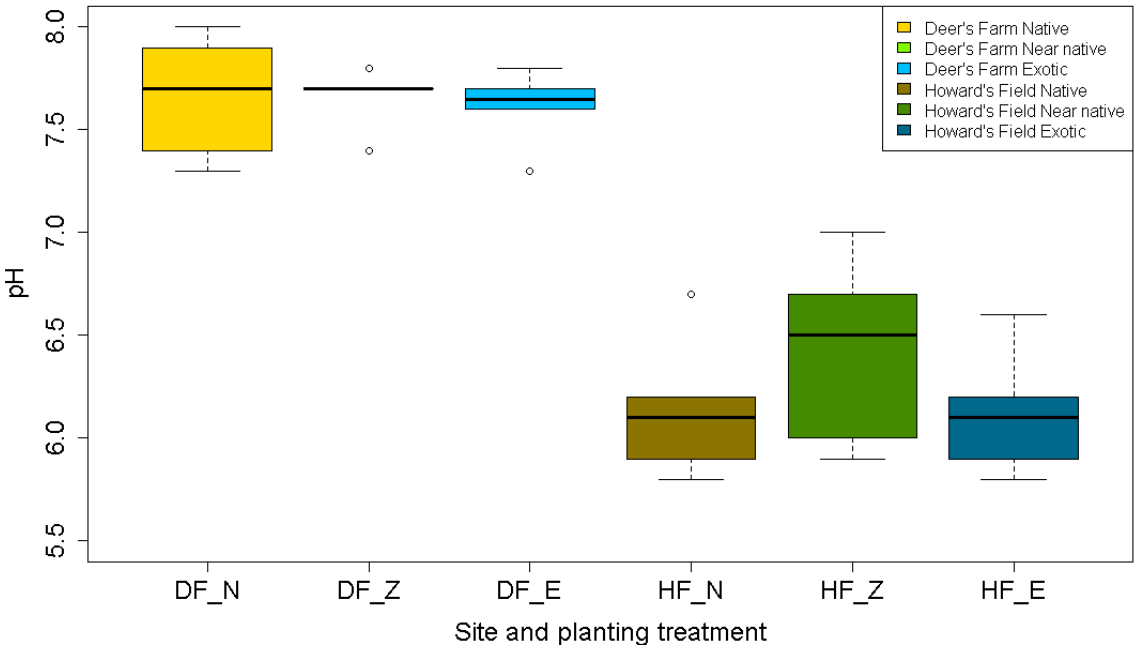

Figure 2.4.1b. Boxplots of pH under each of the treatments at both Deer's Farm and Howard's Field (DF_N: Deer's Farm Native, DF_Z: Deer's Farm Near native, DF_E: Deer's Farm Exotic, HF_N: Howard's Field Native, HF_Z: Howard's Field Near native, HF_E: Howard's Field Exotic), from the 2014 NRM soil analysis.

A two-way ANOVA test revealed no significant difference in pH (NRM laboratories pH values: Table 2., Appendix 2.4.) between the vegetation origin treatments ($F_{2, 30} = 1.425$, $p = 0.256$), H0 was accepted, see Figure 2.4.1b. for a graphical representation of the RHS experimental sites separated by plot treatment.

For all sites the pH values, of the soil samples analysed by NRM laboratories, were significantly different to those obtained from the Roehampton pH analysis: paired T-tests performed in R, see Table 4., Appendix 2.4. for p values and degrees of freedom. The pH values obtained from the Roehampton analysis of the soil cores from which the soil fauna was extracted were significantly more acidic, see Figure 2.4.1c. for a graphical representation.

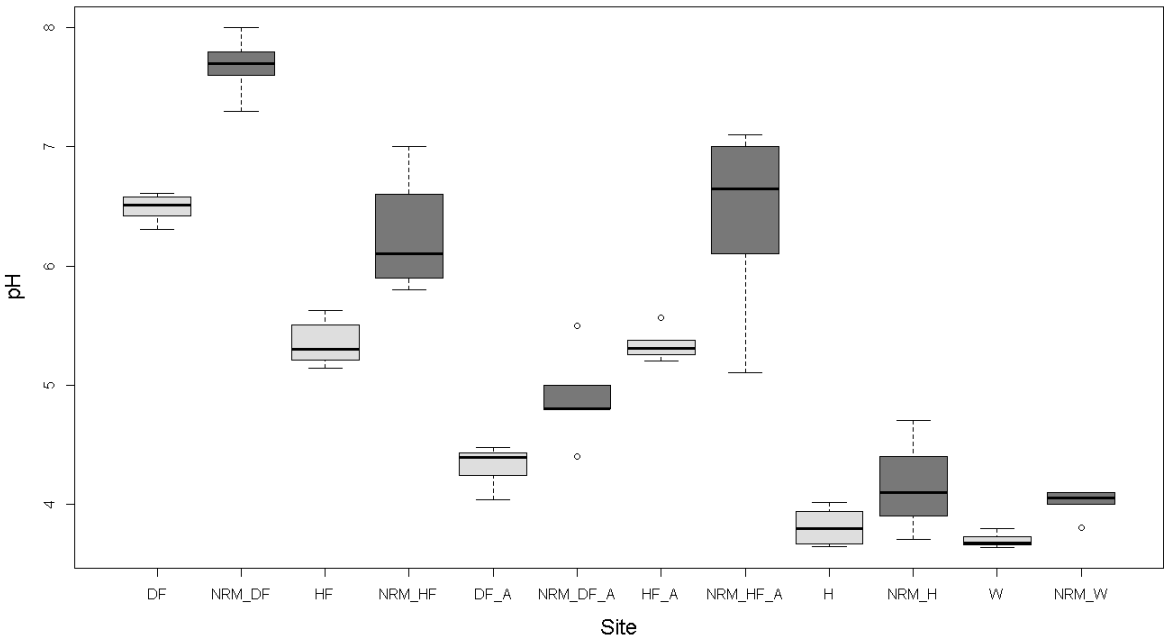

Figure 2.4.1c. Boxplots of pH at each of the sites (DF: Deer's Farm, HF: Howard's Field, DF_A: Deer's Farm adjacent, HF_A: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood). Site codes preceded by the letters NRM are the pH values from the soil analysis by NRM laboratories. Light grey: Roehampton analysis, dark grey: NRM Laboratories analysis.

A Pearson's correlation coefficient was calculated to assess the association between the two sets of soil pH, there was a positive correlation $r = 0.953$, 58 d.f., $p < 0.001$. The relationship between the sites remained the same, i.e. the most acidic soils came from Buxton Wood followed by Wisley Common, then the Deer's Farm adjacent grassland sites, with the Deer's Farm experimental plots being the most alkaline.

In both the NRM pH data set and the soil core pH data set the mean pH of the Howard's Field plots and the mean pH of the Howard's Field adjacent grassland sites were not significantly different from each other (Welch's two sample T-test conducted in R; null hypothesis (H0): $\mu_1 = \mu_2$, alternative hypothesis (Ha): $\mu_1 \neq \mu_2$, $p = 0.83$ with 11.34 d.f. and $p = 0.53$ with 5.79 d.f. for the soil core pH data set and NRM pH data set, respectively, so H0 accepted in both cases).

2.4.2. Magnesium

A Kruskal-Wallis test revealed a significant difference in available magnesium (NRM laboratories values: Table 2., Appendix 2.4.) across all of the sites ($\chi^2 = 48.7$, 5 d.f., $p < 0.001$), H0 was rejected. A post-hoc Dunn test showed where the significant differences between sites lay, see Figure 2.4.2a. for a graphical representation of the available magnesium; the sites with the same letter above them do not differ significantly from each other $p < 0.05$, see Table 5., Appendix 2.4. for the full statistical output.

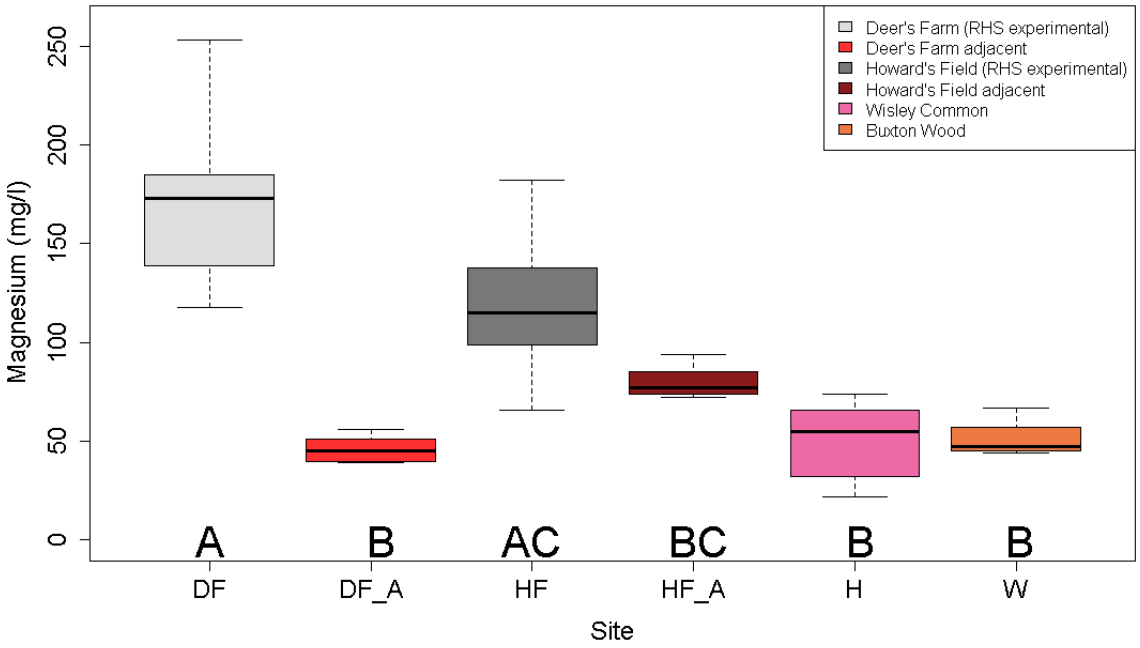

Figure 2.4.2a. Boxplots of available magnesium (mg/l) at each of the sites (DF: Deer's Farm, HF: Howard's Field, DF_A: Deer's Farm adjacent, HF_A: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood), from the 2014 NRM soil analysis. Sites followed by the same letter do not differ according to the Dunn's post-hoc test.

When just the RHS experimental plot data was considered a two-way ANOVA test revealed that there was a statistically significant difference in available magnesium between the Deer's Farm and Howard's Field sites ($F_{1, 30} = 28.186$, $p < 0.0001$) and the vegetation origin treatments ($F_{2, 30} = 3.832$, $p = 0.033$). After a Tukey's HSD test the difference in treatment was found to be between the Native and Near native plots, with the Near native treatments containing significantly more available Mg (p adjusted =

0.037). However, there was an outlier (1.5 times the interquartile range) in the Near native treatment at Deer's Farm, see Figure 2.4.2b. for boxplots of the RHS experimental sites separated by vegetation origin treatment. When this outlier was removed and a two-way ANOVA Type II SS (for unbalanced data) was performed, using the R package "car" (Fox et al. 2014), treatment was no-longer significant ($F_{2, 29} = 2.783$, $p = 0.078$), and there was still a significant difference between the two sites ($F_{1, 29} = 29.369$, $p < 0.0001$).

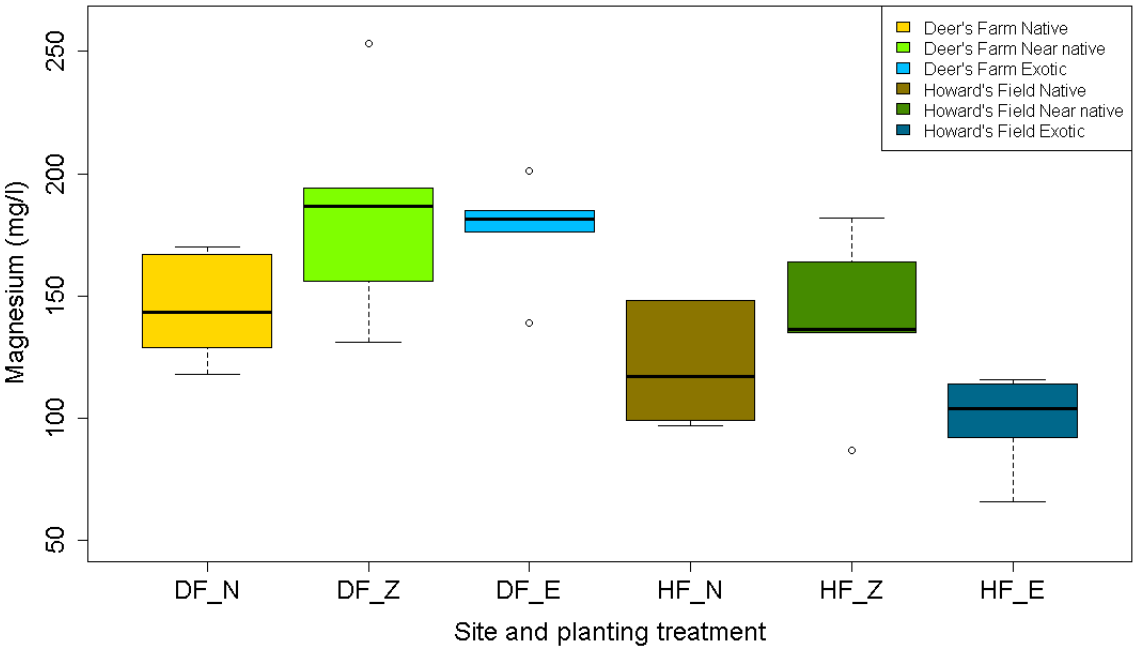

Figure 2.4.2b. Boxplots of available magnesium (mg/l) under each of the treatments at both Deer's Farm and Howard's Field (DF_N: Deer's Farm Native, DF_Z: Deer's Farm Near native, DF_E: Deer's Farm Exotic, HF_N: Howard's Field Native, HF_Z: Howard's Field Near native, HF_E: Howard's Field Exotic), from the 2014 NRM soil analysis.

2.4.3. Phosphorus

A Kruskal-Wallis test revealed a significant difference in available phosphorus (NRM laboratories values: Table 2., Appendix 2.4.) across all of the sites ($\chi^2 = 37.7$, 5 d.f., $p < 0.001$), H0 was rejected. A post-hoc Dunn test showed where the significant differences between sites lay, see Figure 2.4.3a. for a graphical representation of the available phosphorus at each of the sites; the sites with the same letter above them do not differ significantly from each other $p < 0.05$, see Table 6., Appendix 2.4. for the full statistical output.

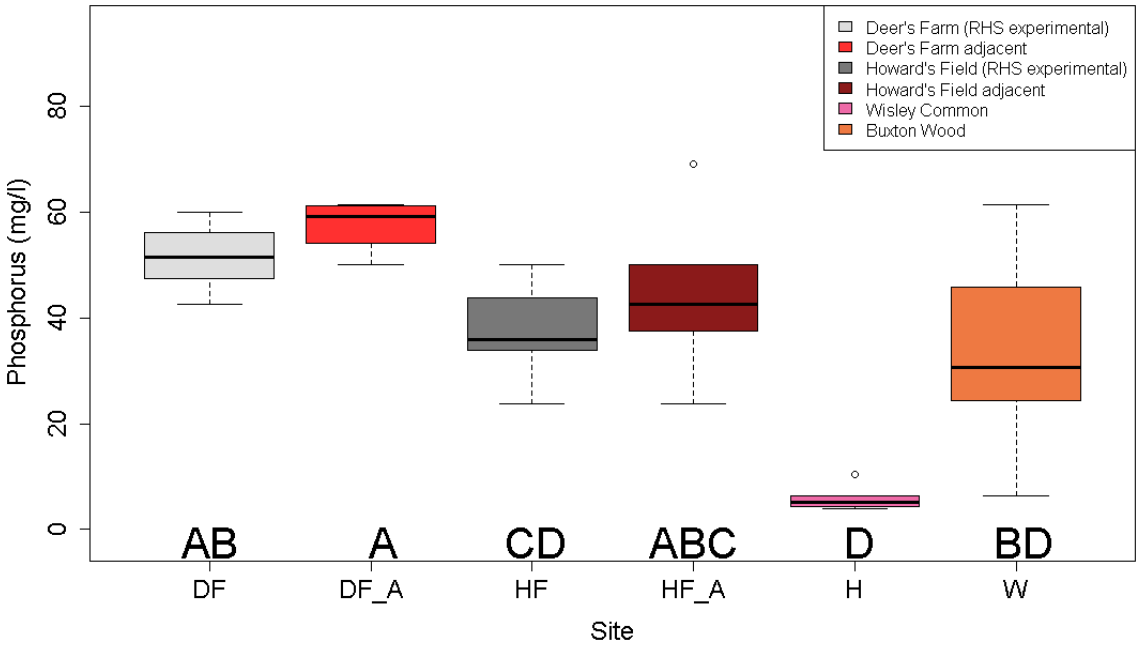

Figure 2.4.3a. Boxplots of available phosphorus (mg/l) at each of the sites (DF: Deer's Farm, HF: Howard's Field, DF_A: Deer's Farm adjacent, HF_A: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood), from the 2014 NRM soil analysis. Sites followed by the same letter do not differ according to the Dunn's post-hoc test.

A two-way ANOVA test also revealed the significant difference between the available phosphorus at the Deer's Farm and Howard's Field RHS experimental sites ($F_{1, 30} = 50.744$, $p < 0.0001$). No significant difference in available phosphorus was found between the vegetation origin treatments ($F_{2, 30} = 3.079$, $p = 0.061$), H0 was accepted, see Figure 2.4.3b. for a graphical representation of the RHS experimental sites separated by plot treatment.

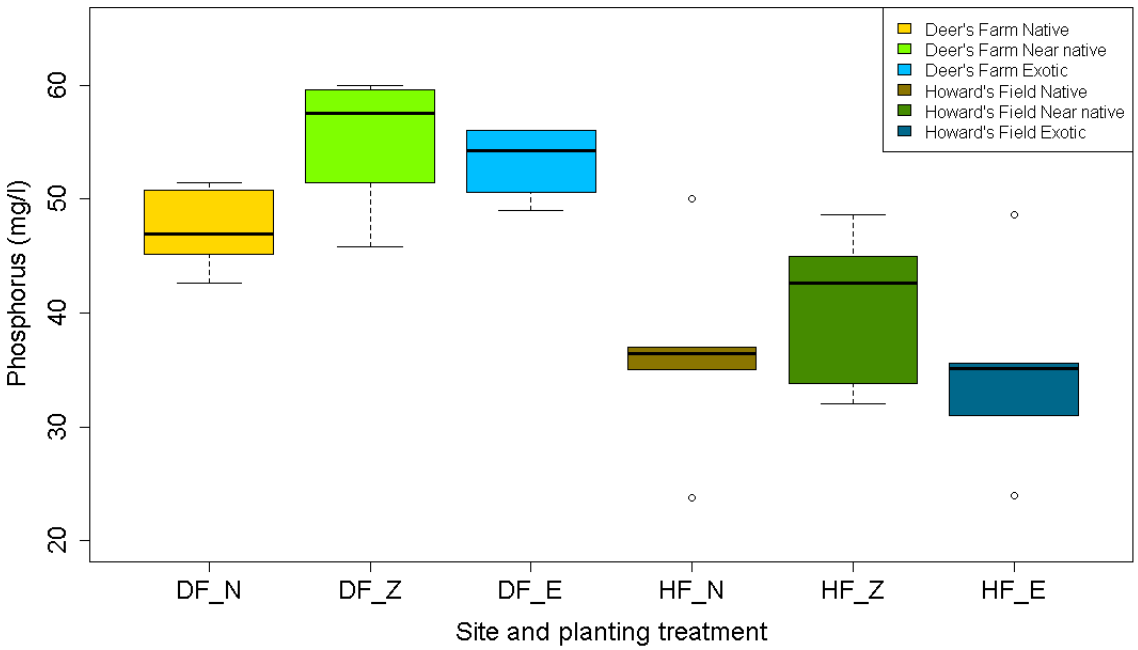

Figure 2.4.3b. Boxplots of available phosphorus (mg/l) under each of the treatments at both Deer's Farm and Howard's Field (DF_N: Deer's Farm Native, DF_Z: Deer's Farm Near native, DF_E: Deer's Farm Exotic, HF_N: Howard's Field Native, HF_Z: Howard's Field Near native, HF_E: Howard's Field Exotic), from the 2014 NRM soil analysis.

2.4.4. Potassium

A Kruskal-Wallis test revealed a significant difference in available potassium (NRM laboratories values: Table 2., Appendix 2.4.) across all of the sites (χ^2 = 32.4, 5 d.f., $p < 0.001$), H0 was rejected. A post-hoc Dunn test showed where the significant differences between sites lay, see Figure 2.4.4a. for a graphical representation of the available potassium at each of the sites; the sites with the same letter above them do not differ significantly from each other $p < 0.05$, see Table 7., Appendix 2.4. for the full statistical output.

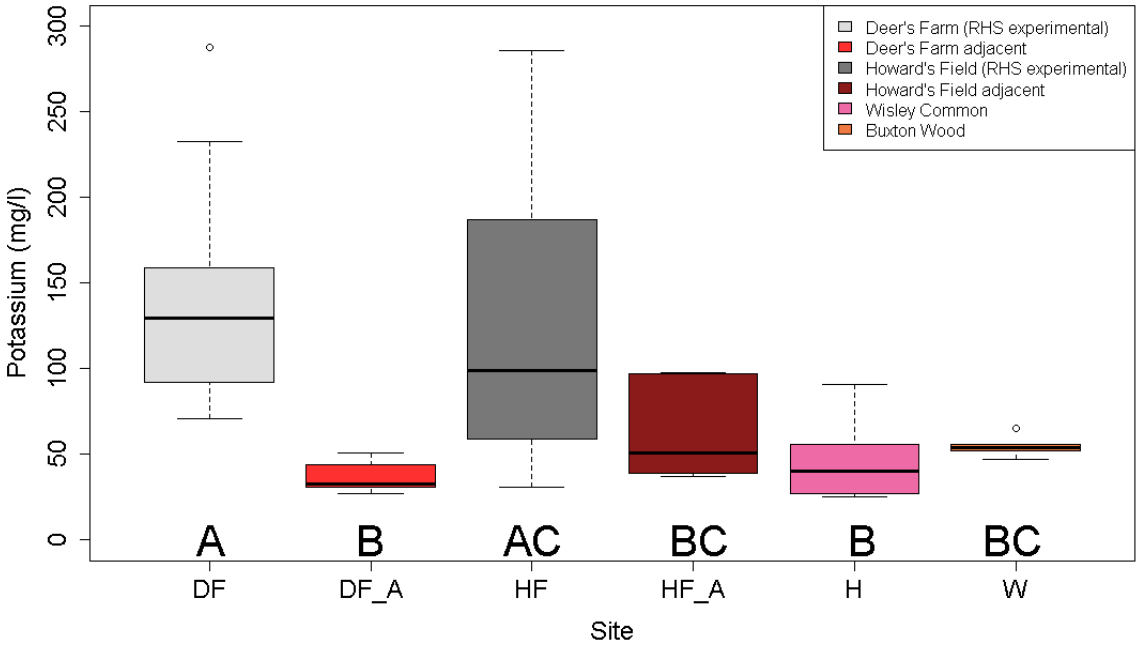

Figure 2.4.4a. Boxplots of available potassium (mg/l) at each of the sites (DF: Deer's Farm, HF: Howard's Field, DF_A: Deer's Farm adjacent, HF_A: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood), from the 2014 NRM soil analysis. Sites followed by the same letter do not differ according to the Dunn's post-hoc test.

A two-way ANOVA test revealed no significant difference in available potassium between the vegetation origin treatments ($F_{2, 30} = 1.491$, $p = 0.241$), H0 was accepted, see Figure 2.4.4b. for a graphical representation of the RHS experimental sites separated by treatment.

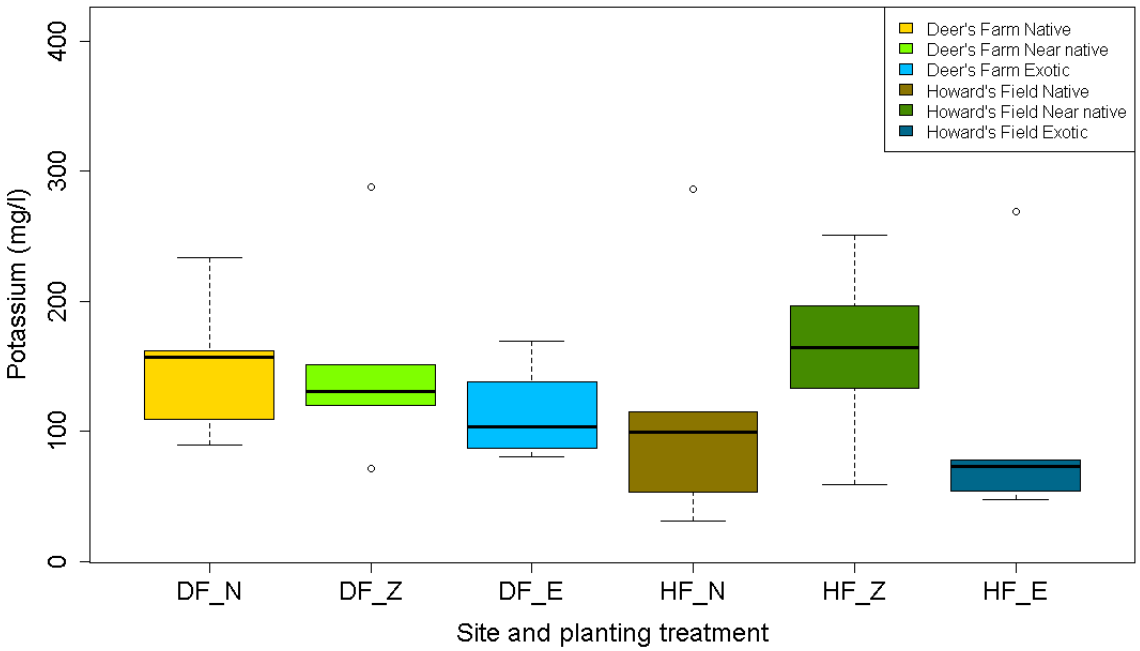

Figure 2.4.4b. Boxplots of available potassium (mg/l) under each of the treatments at both Deer's Farm and Howard's Field (DF_N: Deer's Farm Native, DF_Z: Deer's Farm Near native, DF_E: Deer's Farm Exotic, HF_N: Howard's Field Native, HF_Z: Howard's Field Near native, HF_E: Howard's Field Exotic), from the 2014 NRM soil analysis.

2.4.5. Organic content

A Kruskal-Wallis test revealed a significant difference in loss on ignition (LOI) (NRM laboratories values: Table 2., Appendix 2.4.) across all of the sites (χ^2 = 12.2, 5 d.f., $p < 0.05$), H0 was rejected. A post-hoc Dunn test showed that there were only significant differences in LOI between the Deer's Farm adjacent site and both the RHS experimental plot sites; Deer's Farm and Howard's Field ($Z = 3.07$, $p < 0.05$) and ($Z = -3.17$, $p < 0.05$), respectively, as well as Buxton Wood ($Z = 2.74$, $p < 0.05$). See Table 8., Appendix 2.4. for the full statistical output, Figure 2.4.5a. for a graphical representation of the LOI at each of the sites.

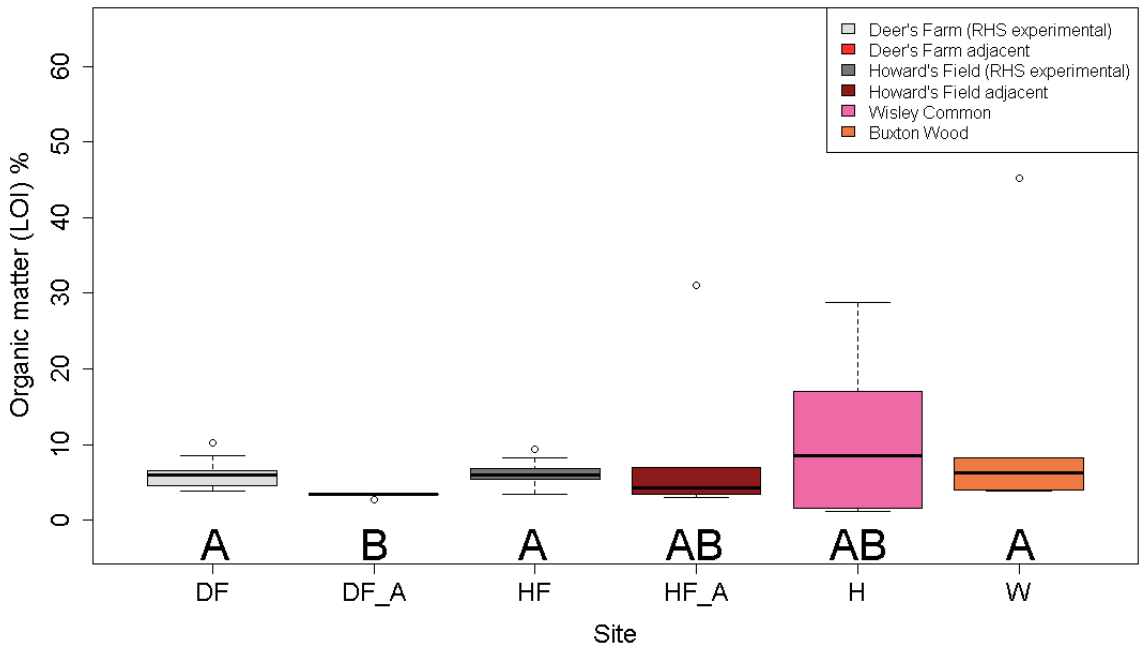

Figure 2.4.5a. Boxplots of LOI at each of the sites (DF: Deer's Farm, HF: Howard's Field, DF_A: Deer's Farm adjacent, HF_A: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood), from the 2014 NRM soil analysis. Sites followed by the same letter do not differ according to the Dunn's post-hoc test.

A two-way ANOVA test revealed no significant difference between the LOI for the Deer's Farm and Howard's Field RHS experimental sites ($F_{1, 30} = 0.025$, $p = 0.875$). No significant difference in LOI was found between the vegetation origin treatments ($F_{2, 30} = 2.022$, $p =$

0.15), H0 was accepted, see Figure 2.4.5b. for a graphical representation of the RHS experimental sites separated by plot treatment.

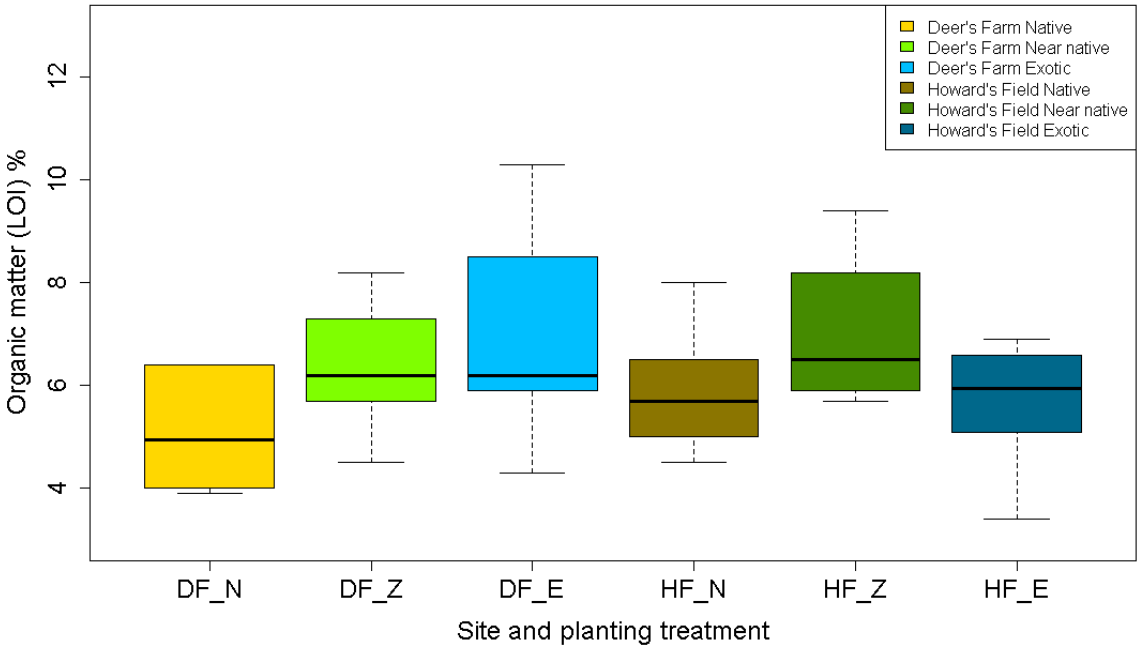

Figure 2.4.5b. Boxplots of LOI under each of the treatments at both Deer's Farm and Howard's Field (DF_N: Deer's Farm Native, DF_Z: Deer's Farm Near native, DF_E: Deer's Farm Exotic, HF_N: Howard's Field Native, HF_Z: Howard's Field Near native, HF_E: Howard's Field Exotic), from the 2014 NRM soil analysis.

2.3.6. Nitrogen

A Kruskal-Wallis test revealed a significant difference in total available nitrogen (NRM laboratories values: Table 2., Appendix 2.4.) across all of the sites ($\chi^2 = 17.9$, 5 d.f., $p < 0.01$), H0 was rejected. A post-hoc Dunn test showed where the significant differences between sites lay, see Figure 2.4.6a. for a graphical representation of the total available nitrogen at each of the sites.

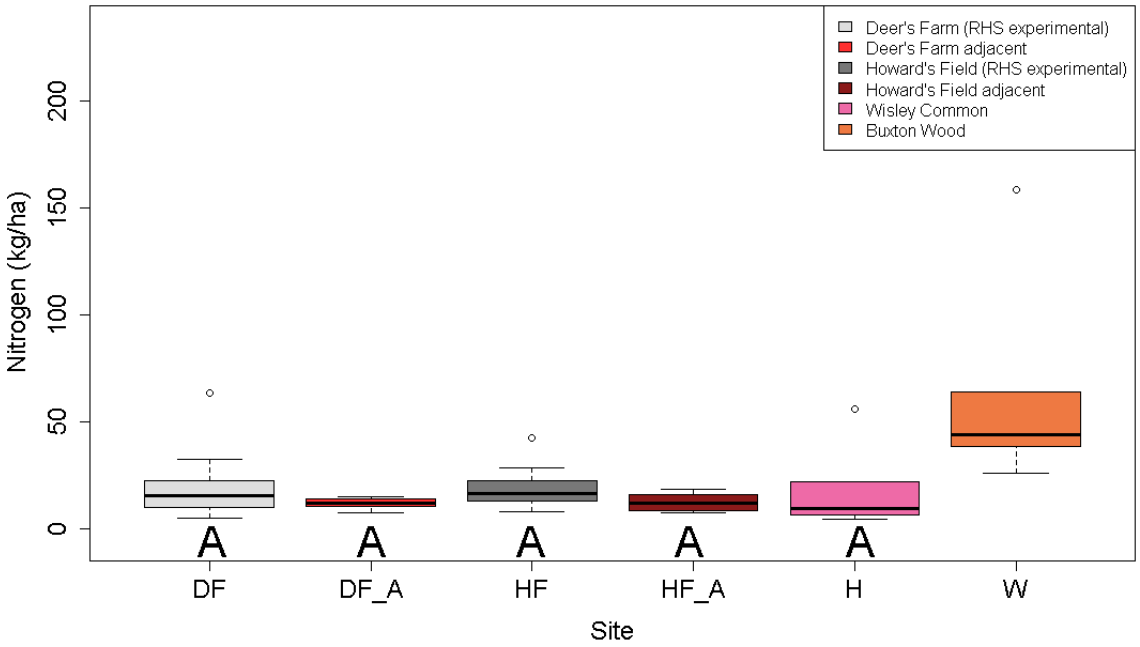

Figure 2.4.6a. Boxplots of available nitrogen (Kg/ha) at each of the sites (DF: Deer's Farm, HF: Howard's Field, DF_A: Deer's Farm adjacent, HF_A: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood), from the 2014 NRM soil analysis. Sites followed by the same letter do not differ according to the Dunn's post-hoc test.

Buxton Wood differs significantly from all the other sites in terms of total available nitrogen $p < 0.05$, see Table 9. (Appendix 2.4.) for the full statistical output, with a mean value of 62.8 ± 19.8 Kg/ha (6.28 ± 1.98 g/m^2). A Kruskal-Wallis test found that ammonium ($NH4^+$) did not differ significantly across the sites ($\chi^2 = 7.72$, 5 d.f., $p = 0.172$), H0 was accepted, see Figure 2.4.6b. for a graphical representation of the ammonium content of the soil at each of the sites. The values for the RHS experimental plots were high, but not significantly different from any of the other sites (aside from Buxton Wood), with mean values of 18.9 ± 3.2 Kg/ha and 18.4 ± 2 Kg/ha for Deer's Farm and Howard's Field, respectively.

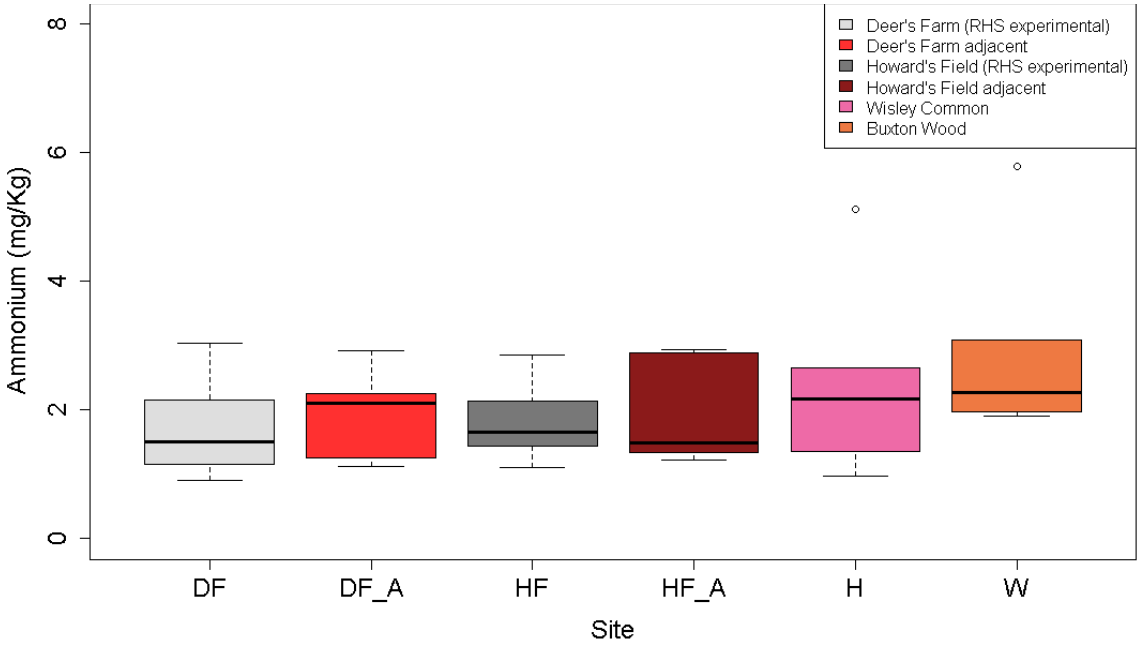

Figure 2.4.6b. Boxplots of ammonium (mg/Kg) at each of the sites (DF: Deer's Farm, HF: Howard's Field, DF_A: Deer's Farm adjacent, HF_A: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood), from the 2014 NRM soil analysis.

A Kruskal-Wallis test revealed that there was a significant difference in nitrate (NRM laboratories values: Table 2., Appendix 2.4.) across all of the sites ($\chi^2 = 24.94$, 5 d.f., $p < 0.001$), H0 was rejected. A post-hoc Dunn test showed where the significant differences between sites lay, see Figure 2.4.6c. for a graphical representation of the nitrate content at each of the sites; the sites with the same letter above them do not differ significantly from each other $p < 0.05$, see Table 10., Appendix 2.4. for the full statistical output.

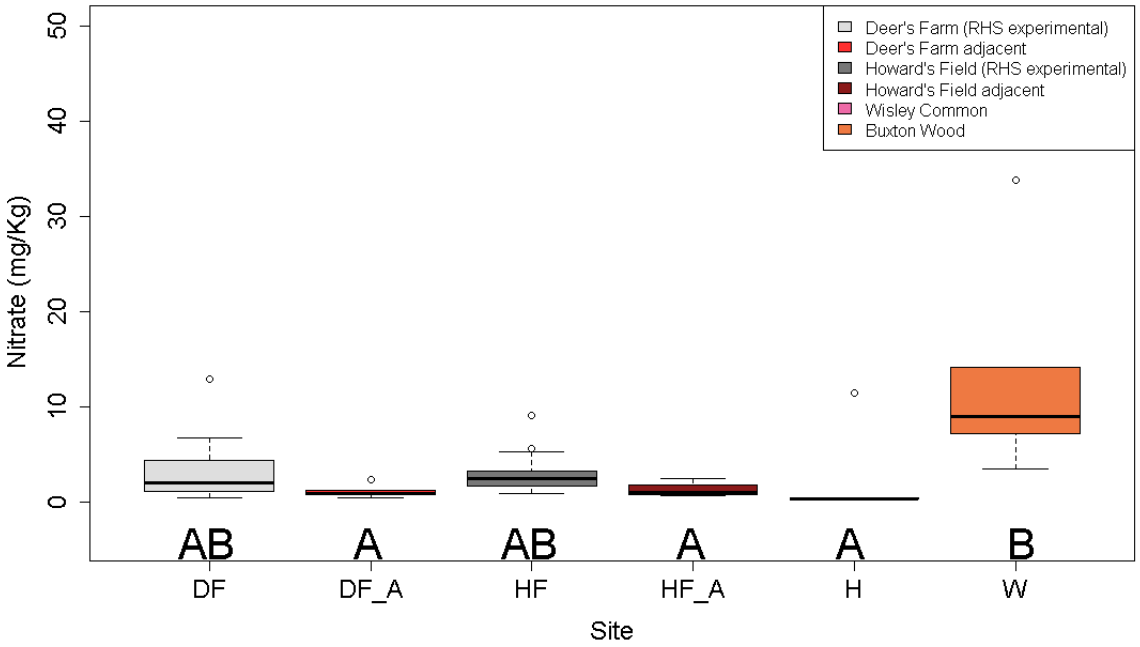

Figure 2.4.6c. Boxplots of nitrate (mg/Kg) at each of the sites (DF: Deer's Farm, HF: Howard's Field, DF_A: Deer's Farm adjacent, HF_A: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood), from the 2014 NRM soil analysis. Sites followed by the same letter do not differ according to the Dunn's post-hoc test.

Within the RHS experimental plots a two-way ANOVA test revealed no significant difference in available nitrogen between the vegetation origin treatments ($F_{2,30} = 0.949$, $p = 0.398$), H0 was accepted, see Figure 2.4.6d. for a graphical representation of the RHS experimental sites separated by plot treatment.

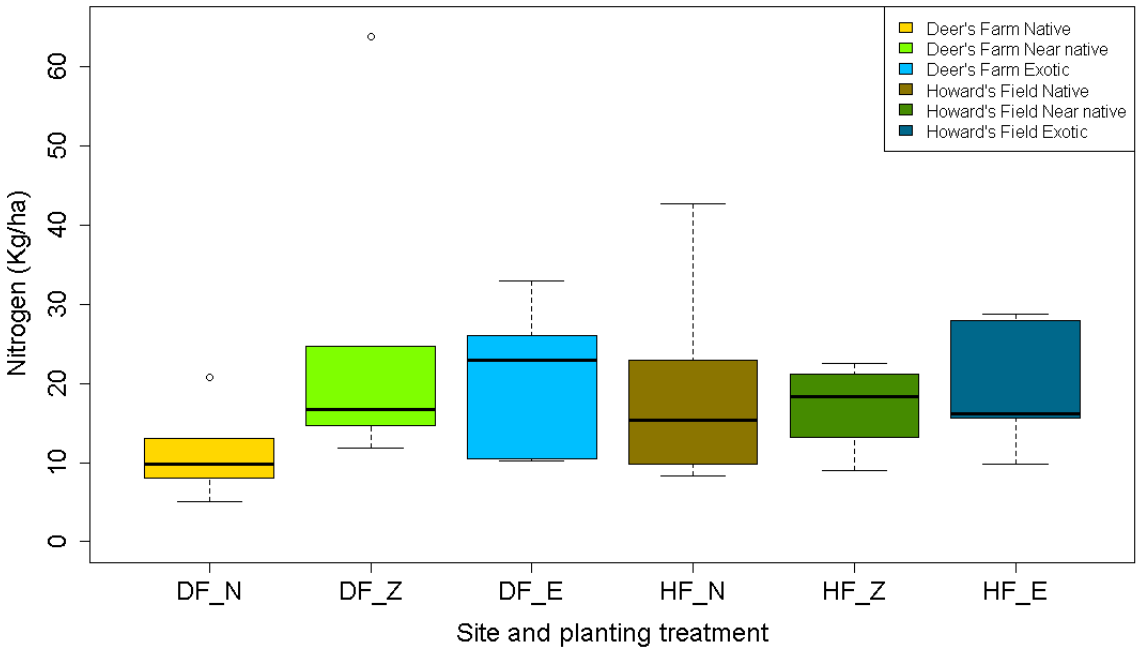

Figure 2.4.6d. Boxplots of available nitrogen (Kg/ha) under each of the treatments at both Deer's Farm and Howard's Field (DF_N: Deer's Farm Native, DF_Z: Deer's Farm Near native, DF_E: Deer's Farm Exotic, HF_N: Howard's Field Native, HF_Z: Howard's Field Near native, HF_E: Howard's Field Exotic), from the 2014 NRM soil analysis.

As would be expected two-way ANOVA tests revealed no significant differences in either ammonium or nitrate content of the soil between the RHS experimental plots ($F_{2, 30} = 1.764$, $p = 0.189$) and ($F_{2, 30} = 1.096$, $p = 0.347$), respectively. H0 was accepted, see Figure 2.4.6e. and Figure 2.4.6f. for graphical representations of the RHS experimental sites separated by plot treatment.

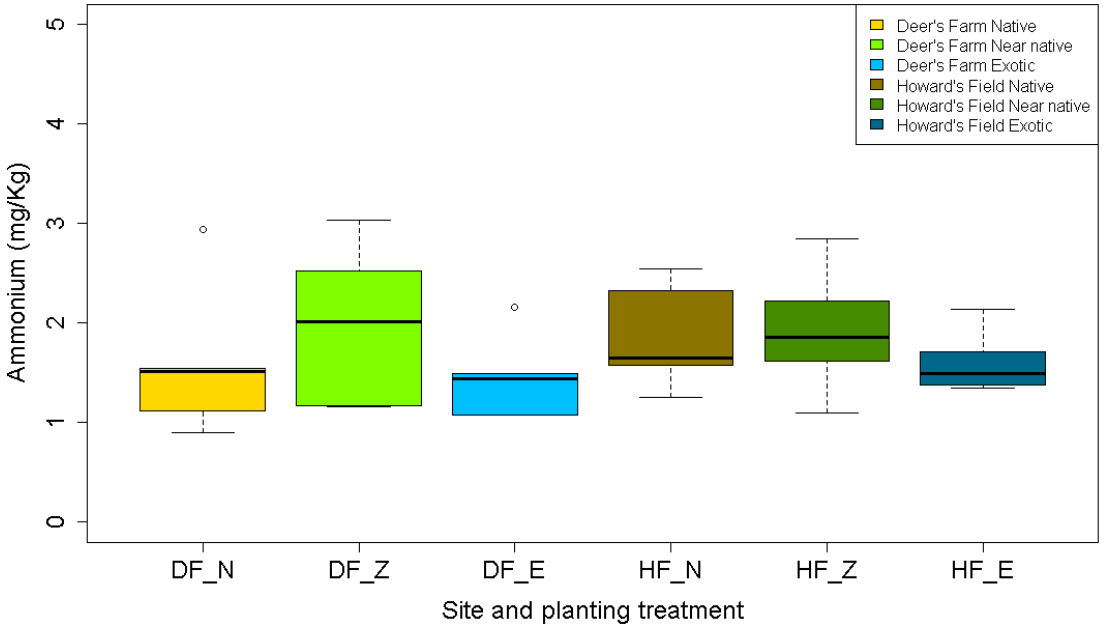

Figure 2.4.6e. Boxplots of ammonium (mg/Kg) under each of the treatments at both Deer's Farm and Howard's Field (DF_N: Deer's Farm Native, DF_Z: Deer's Farm Near native, DF_E: Deer's Farm Exotic, HF_N: Howard's Field Native, HF_Z: Howard's Field Near native, HF_E: Howard's Field Exotic), from the 2014 NRM soil analysis.

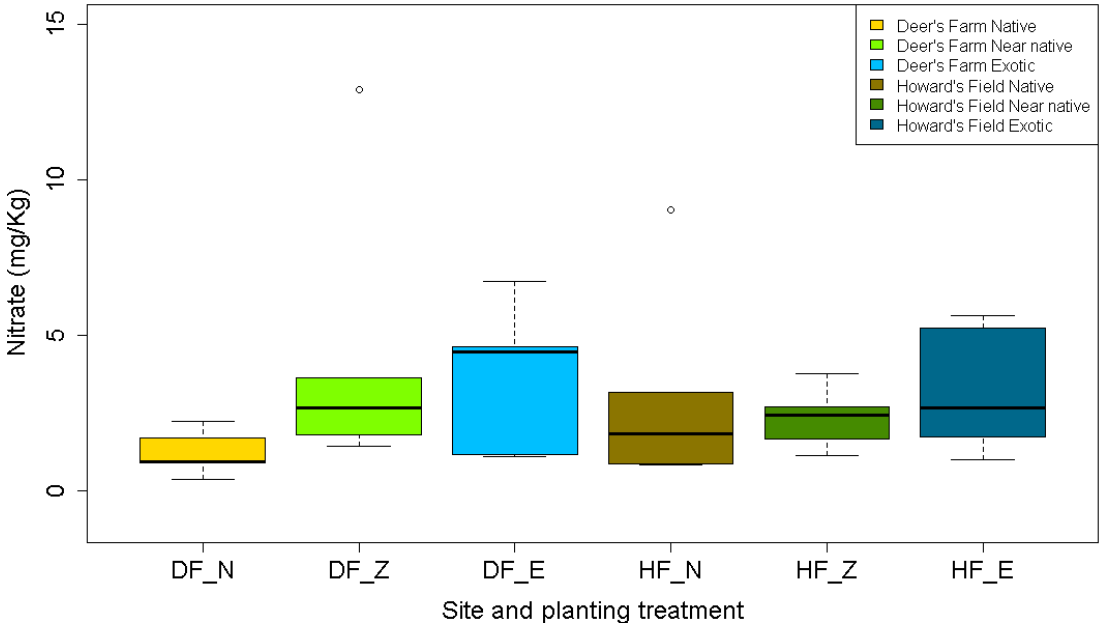

Figure 2.4.6f. Boxplots of nitrate (mg/Kg) under each of the treatments at both Deer's Farm and Howard's Field (DF_N: Deer's Farm Native, DF_Z: Deer's Farm Near native, DF_E: Deer's Farm Exotic, HF_N: Howard's Field Native, HF_Z: Howard's Field Near native, HF_E: Howard's Field Exotic), from the 2014 NRM soil analysis.

Table 2.4. summarises the results of all the soil property parameters measured in this chapter, for both the comparisons between the sites and within the RHS experimental sites for the vegetation origin treatments.

Table 2.4. Table of soil property comparisons, for each parameter sites with the same letter differ significantly according to the Dunn's post-hoc test. For (*) see discussion. Sites; DF: Deer's Farm, DFA: Deer's Farm adjacent, HF: Howard's Field, HFA: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood.

	Treatment	Site					
	(N/Z/E)	DF	DFA	HF	HFA	H	W
pH	NS	ABC	A	BC	D	B	CD
Mg	NS*	ABCD	AE	EF	B	C	DF
P	NS	AB	CDE	AC	F	BDF	E
K	NS	ABCD	AE	EF	B	CF	A
LOI	NS	A	ABC	B	NS	NS	C
total N	NS	A	B	C	D	E	ABCDE
$NH4^+$	NS	NS	NS	NS	NS	NS	NS
$NO3^-$	NS	NS	A	NS	B	C	ABC

NS: no significant differences

2.5. Discussion

2.5.1. pH

The pH values obtained from the semi-natural habitats of Buxton Wood and Wisley Common were acidic, consistent with those expected to be found from Bagshot Sands. Both of the RHS experimental plot sites were less acidic than Buxton Wood and Wisley Common and than when they were previously sampled in 2009 (Deer's Farm: pH 6.3; Howard's Field: pH 5.9), though as mentioned in Phillips and Armitage (2010) fertilisers have been applied across the garden which may account for the raised pH.

The pH of the site adjacent to Deer's Farm was more acidic than the Deer's Farm experimental plots and similar to that of Buxton Wood and Wisley Common. The pH of the site adjacent to Howard's Field was more similar to that of the corresponding experimental plots (i.e. more alkaline), however, it is within the confines of the main RHS

garden. Within both the RHS experimental sites there was no difference in pH of the plots under different vegetation origin planting treatments.

The significant difference in pH values obtained between the NRM laboratories and the Roehampton University soil analysis is most likely due to unavoidable differences in soil sample handling and sample storage. The NRM pH values are likely to be more accurate and indicative of the true pH of the study sites, as there was less handling, however, the pH values from the soil analysis conducted at Roehampton have been used in Chapter 3. when analysing soil fauna abundance and diversity as there is a value that corresponds to each soil core the fauna were extracted from and Chapter 5. for consistency, as the relationships between site and pH remained the same. The pH of each sample prior to the soil handling could be estimated by regression, however, it is not necessary to do this as it would add nothing to the power of the conclusions.

pH is an important co-variate in exploring the soil fauna species compositions as it is known to affect numerical abundance with different species having different preferences and tolerances; Collembola, Oribatid mites and Isopoda pH preferences have been developed as a bioindicator system for soil acidity (Mulder, 2005; Van Straalen & Verhoef, 1997). As the pH differs across the range of sites it is important to include this within the models.

2.5.2. Soil nutrients (magnesium, phosphorus and potassium) and organic content

The soil of the sites differed in the availability of macronutrients, most notably magnesium and potassium where the RHS experimental plots tended to have significantly greater availability of these nutrients especially when compared to the heath site at

Wisley Common and the Buxton Wood site. The 2009 application of magnesium sulphate to the RHS experimental plots at Deer's Farm is still apparent. Originally the levels of available magnesium in the soil there would have most likely been similar to that of the Deer's Farm adjacent site, where the lowest levels, from this soil analysis, were found.

For the RHS experimental sites there was no difference in available phosphorus or potassium under the different vegetation origin planting treatments. However, for available magnesium a difference was found between the Native and Near native plots, after the removal of an outlying data point from the Near native treatment at Deer's Farm there was no-longer any difference between treatments. The data point may have been the result of uneven application of Mg over the site at Deer's Farm. For the soil analysis one sample was collected from each plot (six per treatment at each of the RHS experimental sites) but over the duration of this research twelve soil cores were taken from randomly selected points within each of the plots and will probably cover the full range of available Mg values there.

In terms of organic content of the soils, the sites were not significantly different from each other aside from the Deer's Farm adjacent site which had a significantly lower organic content than some of the other sites; this is consistent with the soil profile photo taken which showed no O horizon (Figure 2.1.3a.). From these samples there was greater variability at some sites than others: Buxton Wood and Wisley Common. Within both the RHS experimental sites at Deer's Farm and Howard's Field there was no significant difference in organic content of the soil under the different vegetation origin planting treatments.

2.5.3. Nitrogen

There was no difference in total available nitrogen (or either ammonium ($NH4^+$) or nitrate ($NO3^-$) when they were analysed separately) between the different vegetation origin treatments or the two RHS experimental sites. Across all sites the main difference in total nitrogen availability was at Buxton Wood, which contained levels significantly higher than all the other sites. A possible explanation could lie in Buxton Wood's proximity to the M25 (a major motorway encircling London); whilst no difference was found in $NH4^+$ there were significant differences in $NO3^-$, between Buxton Wood and all sites apart from the RHS experimental plots. Nitrate levels and nitrification have been found to be positively related to the number of roads within 1 km of sites (whilst ammonium concentrations increased with increasing distance from the roads) (Manninen et al. 2013). NOx present in vehicle exhaust fumes can be deposited, the main constituent emitted is NO2, which after atmospheric oxidation produces nitric acid and $NO3^-$, leaching or utilisation of available N can also cause acidification of soils. It could be that the soil of Buxton Wood has reached nitrogen saturation: with availability of $NH4^+$ and $NO3^-$ in excess of the combined plant and microbial nutritional demands, resulting in accumulation (Aber et al., 1989). Additionally the Buxton Wood site has not been subject to recent landuse change or disturbance, which may have lead to a more stable system tending towards a saturation situation; conversion from forest to agricultural management has been associated with nitrogen loss from soils as a result of cultivation and disturbance (Roy & Misra 2005). The available nitrogen at the other sites is more likely to have become depleted. The nitrogen and other macronutrient data has been used in the discussion of Chapter 5. in relation to decomposition.

2.6. Conclusions

As there are differences between the sites, especially with regards to pH which has been shown to be an important factor in the distribution of soil fauna (see Chapter 1., Section 1.7.1.), this was built into the models (pH) and the differences in the availability of the macronutrients (including nitrogen) and organic content are discussed when comparing the soil biodiversity and ecosystem function of the sites. With one explainable exception no statistically significant difference was found in the soil properties of the RHS experimental plots subject to the different vegetation origin planting treatments.

Chapter 3. Soil fauna abundance and taxonomic diversity

3.1. Introduction

As discussed in Chapter 1., Section 1.5., there are several parameters that can be used to characterise and assess soil biodiversity. Here data are presented on the numerical abundance of all taxa encountered. A selection of soil fauna taxonomic groups have been compared across the different sites and treatments in terms of their abundance and density (Acari and Collembola), with comparisons in taxonomic diversity for the Collembola which were identified to species level.

In order to assess the soil community, soil samples first needed to be collected from each plot and the fauna extracted. There has been discussion regarding appropriate sampling depths for soil fauna studies as different soil organisms inhabit different layers of the soil profile. Earthworms are divided into ecological groups based on the soil layer they inhabit and their burrowing behaviour (Lavelle, 1988) and different Collembola species are known to be found at differing depths (Hopkin, 1997) at varying abundances (Berg, et al., 1998).

On reviewing the literature, André *et al*. (2002) found several estimates of the soil depth in which 50% of animals were living (termed SD_{50}) to be greater than 10 cm, however, on inspection of the studies reviewed, the majority were from biomes/climates very different to the study sites here, with the closest site; a meadow at Le Pin-au-Haras (France) supplying a microarthropod SD_{50} estimate of 6 cm, a Collembola estimate of 8 cm and Acari taxa estimates of 1-9 cm (André et al. 2002), the vertical distribution of taxa was noted to be unimodal with a topsoil mode. This observation is supported by Bardgett

et al. (1993) who found that 92-98% of Collembola and Acari were retrieved from the top 2 cm of soil, with this density distribution corroborating the work of Petersen and Luxton (1982) and Shaw (1985) who also found that the abundance of many Collembola decreased with increasing depth (Shaw retrieving 90% of Collembola from the top 3 cm of the soil profile).

Berlese-Tullgrens (Tullgrens) have been an established method of soil mesofauna extraction, their efficacy has been reported within the literature since their conception in 1905 and subsequent development (Berlese 1905; Tullgren 1918; Ford 1937; Murphy 1962). In 2002 they were the most common method of soil fauna extraction (André et al. 2002) and their use is still prevalent. Tullgren extraction was used for the national survey of soil invertebrates conducted as part of the Countryside survey 2000 (Black et al. 2003) and has subsequently been employed in many other soil fauna studies (e.g. De Deyn et al., 2003; Mulder & Elser, 2009; Mulder, Van Wijnen, & Van Wezel, 2005).

There are alternative methods available including passive hand sorting and floatation in a variety of solutions as well as other dynamic methods (high gradient funnels and canisters). Efficiency is the primary concern with regards to both extraction and time. The passive hand sorting and counting methods tend to be more efficient at extracting soil fauna, however, they have a reduced efficiency time-wise; whilst Tullgrens do generally have lower extraction efficiencies than hand sorting, they are still better than other active methods (André et al. 2002; Coleman & Wall 2007). For leaf litter, Winkler bags are another commonly used method. Work has been done to assess the efficiency at extracting macro-invertebrates, which suggested that longer periods would be required

than is necessary for Tullgren extraction (Krell et al. 2005) and Winkler bags have also been shown not to be a suitable method for Collembola (Shaw & Ozanne, 2011).

Here the soil mesofauna biodiversity is examined, other studies such as Nuria et al. (2011) consider macro-invertebrates as indicators of soil quality, but they sampled 25 cm x 25 cm squares to a depth of 20 cm. For the RHS experimental plots this would have been too destructive, over the duration of the study this would have meant over 8% of the soil surface being removed and with the vegetation, edges, pitfall traps and litterbags this was not feasible and would have interfered with the experimental design and protocols already in place.

Both pH and soil moisture content are commonly included co-variates in soil fauna studies and they have consistently been found to significantly influence faunal composition when included in models (e.g. Chauvat et al., 2007; Mulder et al., 2005). See Chapter 1. Section 1.7.1. for literature on the relationships between soil fauna and pH. Soil fauna are also known to be susceptible to desiccation, with soils classified as dry usually contain the lowest densities (Petersen & Luxton 1982), and so soil moisture is also an important variable. Within the Collembola, different species have differing tolerances to reduced soil moistures via a range of morphological, physiological and behavioural adaptations (Hopkin, 1997 and references therein). Protection is afforded through thickened cuticles and respiratory adaptations: the Actaletoidea and some of the Symphypleona (Sminthurinae) respire through tracheae, so they are less susceptible, whereas other species are atracheate, with the body surface being used for gaseous exchange (Hopkin, 1997; Swift, Heal, & Anderson, 1979). These adaptations are reflected in the criteria that separate Collembola into epiedaphic vs euedaphic species (see Lavelle

& Spain, 2005). There is evidence of correlations between Collembola abundance and soil moisture; abundance decreases with increasing depth and decreasing moisture content (Poole 1962). Increases in microarthropod abundance at the soil surface have been observed following periods of rainfall when soil moisture content is correspondingly greater, especially for sites where conditions are normally dry (Greenslade 1981). The species diversity of euedaphic Collembola has been shown to be positively related to soil water content (Chauvat et al. 2007), so it was important for data on this parameter to be collected.

3.2. Methods

3.2.1. Sample collection

Commencing in July 2011 two sets of samples per plot were collected three times a year; in spring (April), summer (July) and autumn (October), until April '13. This provided several annual comparison points and captured some of the seasonal variations of abundance in the mesofauna, though samples were not collected in the winter due to the lower numbers expected (see Usher, Booth, and Sparkes (1982) and Chapter 1. Section 1.7.3.). For the first period of data collection (July '11) samples were only collected from the RHS experimental plots and adjacent areas, for all other sampling occasions (October '11, April '12, July '12, October '12 and April '13) additional samples were collected from Buxton Wood and Wisley Common. The Deer's Farm adjacent site was originally situated on the north side of the Deer's Farm RHS experimental plots and this is where the July '11 samples came from for this site, however, due to disturbance from construction this was moved to the South side for subsequent sampling occasions. See Chapter 2. for site descriptions and the analysis of their soil properties.

Each RHS plot is 3 m by 3 m, with a pitfall trap permanently set out in the centre, separated from neighbouring plots by a 1 m path. As the number of species encountered is proportional to a power of the area sampled (MacArthur & Wilson 1967) it is important that where sites are compared they are done so over the same area, so all the 'Adjacent', 'Heath' and 'Wood' plots were also placed under the same dimensional constraints (also 3 m by 3 m).

A soil corer 5 cm in diameter was used to sample to a depth of 10 cm at a randomly selected point in each of the plots. These co-ordinates of the random points were generated by rolling percentile dice and avoided major roots, edges and, in the RHS experimental plots, the pitfall traps already set up at the centre of each plot (see Figures 1.-7. Appendix 3.2. for figures of site layouts and soil core sampling location). This soil core diameter was selected because it is a standard size used in similar studies (e.g. Chauvat, Wolters, & Dauber, 2007) and was used to extract soil cores to a sampling depth of 10 cm. Upon collection each sample was wrapped in plastic film to prevent desiccation and microarthropod escape. For each site the samples were collected and extracted on the same day. Berlese-Tullgren funnels, as described by Murphy (1962), were used to extract the soil fauna over a 48 hour period. See Figure 3.2.1. for a diagram of the extraction set up and Figure 3.2.2. for an image of the Tullgren funnels used. Due to the gauge of the holes in the Tullgren mesh earthworms were unable to pass through.

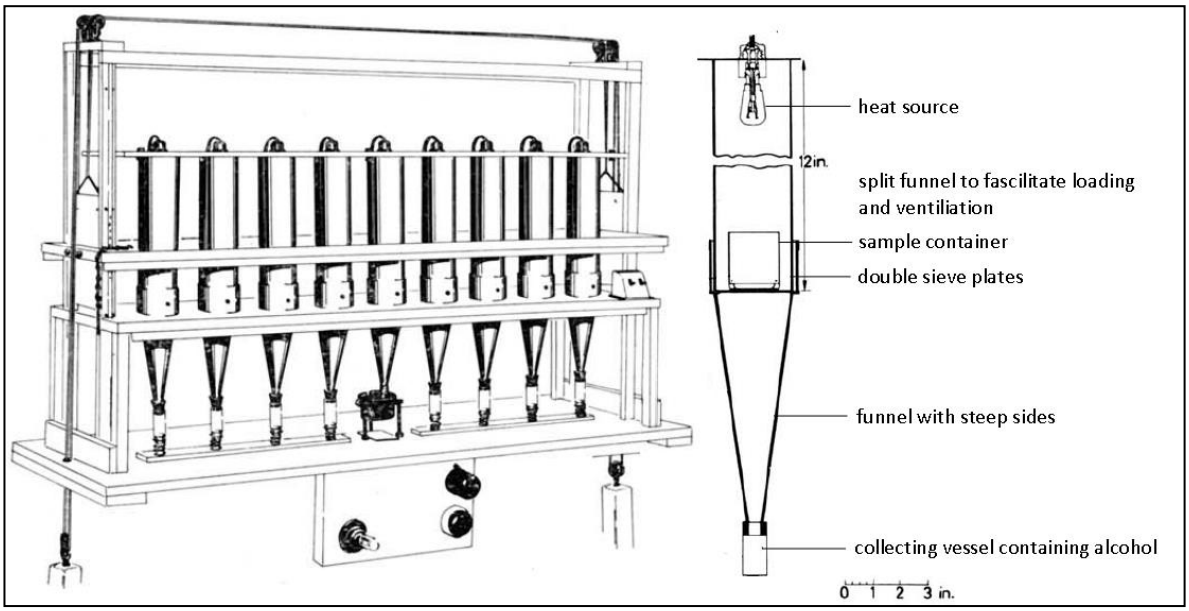

Figure 3.2.1. Tullgren set-up, diagram adapted from Murphy (1962).

Figure 3.2.2. Three of the Tullgren funnels used to extract soil fauna for this study. Photograph adapted from one provided courtesy of the RHS (Bostock, 2011).

The soil fauna were extracted into labelled plastic collection tubes filled with either industrial methylated spirits (IMS) (July ’11) or 100% molecular biology grade ethanol (October ’11, April ’12, July ’12, October ’12 and April ’13), as there was no intention to use the July ’11 samples for molecular work. Parafilm was used to seal gaps between the

stem of the funnel and mouth of the tube to reduce alcohol evaporation and prevent arthropod escape. Soil was retained and dried in an oven at 105 °C for 48 hours and then weighed and dry mass recorded. The soil was temporarily stored at room temperature until the end of each sampling occasion and then transferred to the freezers at the University of Roehampton for long term storage (-20 °C). The collection tubes were taken back to the laboratory at the University of Roehampton for sorting and identification.

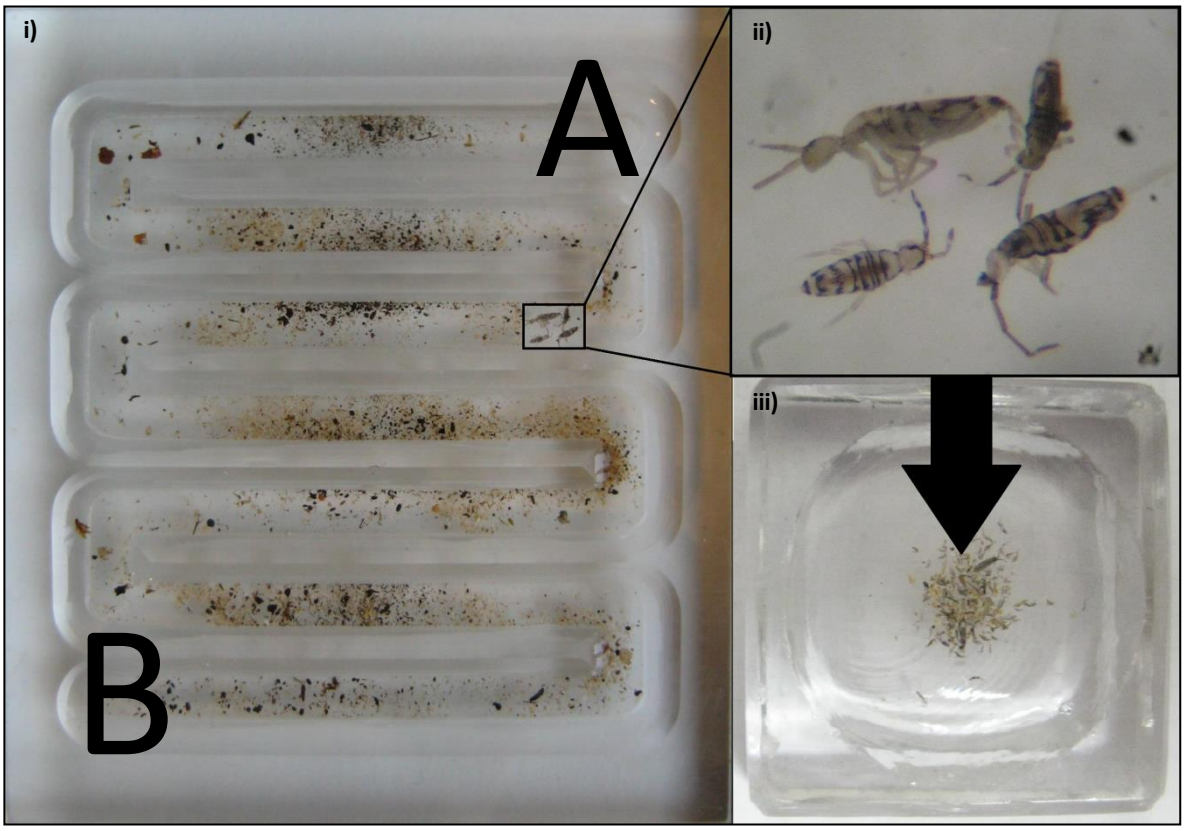

Figure 3.2.3. Bogorov tray set up: i) tray moved underneath a dissecting microscope field of view from point A to point B. ii) Soil fauna removed as encountered and iii) transferred to a watch glass for identification.

A Bogorov tray (a perspex tray with 7 parallel grooves, based on Bogorov (1927), also see Gannon (1971)), was placed under a binocular dissecting microscope, to separate soil fauna from any soil material that passed through the Tullgren meshes. Although more commonly employed in processing meiofauna in aquatic sediments, it was found to be less cumbersome than a petri dish and in my opinion provided greater certainty that no individuals were missed (see Figure 3.2.3.).

3.2.2. Soil fauna identification

Aside from the Acari, all the soil fauna extracted were identified, in addition to being counted, to at least Order, and Family where possible, using Tilling (1987). The Collembola were counted and identified to species primarily using Hopkin (2007) with reference to many other sources (including: Bretfeld, 1999; Dunger & Schlitt, 2011; Fjellberg, 1998, 2008; Jordana, 2012; Potapow, 2001; Thibaud, Schulz, & da Gama Assalino, 2004; Zimdars & Dunger, 1994). Unwin (1988) was used to identify the Coleoptera with reference to Forsythe (2000) and Luff (2007). For other taxa the following keys were used: Diplopoda, Lee (2007); Chilopoda, Barber (2008); Oniscidea, Hopkin (1991); Thysanoptera, Kirk (1996). The Endopterygota larvae, aside from the Elateridae, were identified to Order.

For the reasons discussed in Chapter 1. Section 1.3.2. namely abundance/dominance in soil ecosystems, relative ease of identification and prevalence of study within the literature the Collembola were preferentially identified to species level. Where required, specimens were either cleared and mounted using lactic acid or cleared using a 10% sodium hydroxide solution, transferred to distilled water, the concentration of ethanol gradually increased to 100%, then transferred to clove oil before being permanently mounted in Euparal (see Hopkin, 2007, for the procedure). This is necessary to see the mouthparts (i.e. teeth on the maxillae, molar plate, mandible presence and shape) and enables the chaetotaxy, post antennal organ arrangement and pseudocelli position to be determined more easily, however, it does render specimens unusable for molecular work; DNA extraction.

Some species were pooled at the genus level where identifications would have taken too long either due to the number of individuals or the length of time it would take to observe the required characters.

Mesaphorura spp. were grouped as positive identification is based on chaetotaxy so specimens need to be cleared to be more sure of identification. High numbers of this genus were retrieved and so this would have been too time consuming to do for every specimen. According to Hopkin (2007) the most common species is *M. macrochaeta* and at least one individual was cleared from every soil core and indeed this was the only species encountered.

Protaphorura spp. were pooled under *Protaphorura armata* 'group' as separation between *P. armata*, *P. aurantiaca* and *P. macfadyeni* is based on pseudocelli number/position (Hopkin, 2007) which requires clearing to see with any degree of ease. There are also currently questions regarding the reliability of the pseudocellar species as described in Gisin (1960), with species delimitation issues throughout the genus (Shaw, Faria, & Emerson, 2013). A sufficient number of cases of individuals have been recorded (Hopkin & Shaw, 2014; Hopkin, 2007) and also personally observed, where the pseudocelli arrangement is asymmetric leading the two halves to key to different species.

Folsomia quadrioculata and *F. manolachei* were pooled under *F. quadrioculata* 'group' as determination between them is time consuming because it is based on characters that need to be checked individually under a high power compound microscope (ratio of the length of the longest setae at the end of the abdomen to the mucro and the exact position of one sensilla on second thoracic segment).

Friesea species were also grouped under *Friesea* spp. as some samples contained a mix of three *Friesea* spp.: *F. claviseta*, *F. mirabilis* and *F. truncata*, and because determination between the latter two is relatively time consuming they were grouped. Individuals in the genus *Isotoma* were pooled as separation between *I. anglicana* and *I. viridis* can be time consuming as it is based on whether specimens have one or two pairs of manubrial teeth.

Due to the high soil fauna abundances encountered in the soil cores obtained from the grassland plots in July '11 and October '11, the decision was reached that for the remaining sampling occasions (April '12, July '12, October '12 and April '13) at these sites the soil fauna from only one of the two samples collected would be randomly selected to be processed.

3.2.3. Co-variate data collection

At each sample location, the soil moisture (percentage volumetric water content) was measured using a Delta HH2 moisture meter and a Delta SM200 soil moisture sensor (Delta-T Devices Limited, Cambridge, UK), for mean readings for October '11, April '12, July '12, October '12 and April '13 see Table 1., Appendix 3.2. For the July '11 sampling occasion it was not possible to record soil moisture levels, however, soil moisture data was collected by Salisbury, et al. (2015) in June '11 and August '11 and an average of these two values was used any models that include the first sampling occasion of the RHS experimental plots. Weather data (rainfall) was also retrieved from the Deer's Farm weather station, for the periods coinciding with the sampling occasions (Table 2., Appendix 3.2.). A research assistant, Michael Terrington, was employed to conduct the pH testing on the soils retained from the sample collection, see Chapter 2., Section 2.2.2. for the methods used.

As part of the 'Plants for Bugs' project, estimates of proportion of vegetation cover were collected by Sarah Al-Beidh, Helen Bostock and volunteers at the RHS experimental plot. This was achieved by superimposing a grid onto overhead shots of each plot and then counting all squares at least half-filled with vegetation (Table 3., Appendix 3.2.).

3.3. Analysis

For the 'Plants for Bugs' project only the taxonomic or functional groups where at least 400 individuals were recorded were analysed (Salisbury et al., 2015). As expected from reviewing the literature (see Chapter 1., Section 1.3.2.) the only taxonomic groups that fulfilled that criterion in this dataset were the Collembola and the Acari. Other studies (e.g. Mulder et al., 2005) have pooled species groups into broader taxocenes for analysis, but here the abundances of the remaining taxa were low and the groups would have to have been so broad as to render comparisons meaningless. Neeson, Van Rijn, & Mandelik (2013) discussed the merits and appropriateness of using higher taxon groupings suggesting that for insects, results are less reliable due to greater species diversity.

Studies into soil fauna communities generally compare taxon abundance per unit area or taxon density. As for the April '12, July '12, October '12 and April '13 sampling occasions for the adjacent amenity grassland site only one of the two soil cores collected was processed this meant that the resultant abundances came from differing volumes/dry masses of soil (Kruskal-Wallis: $\chi^2 = 59.01$, 5 d.f., $p < 0.001$). To account for this it was decided that it made the most sense to compare densities of the soil fauna per unit of dry mass or include total soil dry mass as a term in exploratory models that included all sites. To obtain the density of the Collembola and the Acari per kilogram of dry soil mass, the raw abundance figures of Collembola and Acari (see Table 1. of Appendices 3.4.2. and

3.4.3. for full total abundance data) were divided by the soil dry mass (g) of the core they were extracted from and multiplied by 1000, to provide Collembola kg-1 and Acari kg-1, respectively. These data have been used in the graphs so that the different sites can be visually compared.

3.3.1. Generalised linear models

All statistical analysis was conducted in RStudio (RStudio, 2014), versions "Roasted Marshmallows", "Warm Puppy" and "Spring Dance". The R package 'car' (Fox et al. 2014), available on the comprehensive R archive network (CRAN), was used to produce scatterplot matrices of pairwise relationships between the variables prior to analysis. None of the dependent variable data fitted the normal distribution (Gaussian). Within ecological literature it has been commonplace to apply log-transformations to count based data, but see O'Hara and Kotze (2010) for a discussion on the merits of using generalised linear models (GLM) and the actual data distributions instead of performing log-transformations to normalise prior to analysis by general linear models (which assume normality). GLMs were built for both the Collembola and the Acari datasets using the R core package 'stats' (Chambers & Hastie 1992). Starting global models were explored using both the density kg-1 of the selected taxonomic group and the numerical abundance as the dependent variable.

Link functions were explored for the relevant data distributions and a starting model was selected, where possible, based on the Akaike information criterion (AIC); quasi-models do not report likelihoods (although there are workarounds (Bolker 2014)). AIC values provide a measure of the efficiency of the model and the adjusted R^2 value gives the proportion of variance in the dependent variable that has been explained by the model.

This was followed by step-wise deletion of non-significant terms, removing highest order interaction terms first if non-significant, using the 'drop1 function', until only significant terms remained. The resulting models were validated and the assumptions checked at each stage.

For the RHS experimental plot models, abundance was the dependent variable, with 'site' (Deer's Farm or Howard's Field), 'treatment' (vegetation origin: Native, Near native or Exotic), 'planting mix' (A, B or C) and 'season' (April: spring, July: summer, October: autumn (all sampling occasions)) included as independent variables. 'planting mix' was nested within 'treatment' as the planting mixes were not directly comparable; 'Native A' was no more equivalent to 'Exotic A' than it was 'Exotic B'. 'pH' and 'soil moisture' were included as co-variates. As it is vegetation origin that is of the most interest here, all the 'treatment' two-way interactions were included in the full starting models, as well as those between soil moisture and site, and soil moisture and season. It is advised that the total number of terms, including main effects and interaction terms should not be greater than n/3 with some statisticians recommending a maximum of n/10 (Thomas et al. 2013). The number of terms in the models used here does not exceed this.

It was decided to omit vegetation cover from the models because, in my opinion, the dates the overhead shots were taken were not close enough to the sampling occasions, vegetation cover can change considerably over the course of a month, especially in the spring or autumn months. Despite this for two of the sampling occasions (April '12 and October '12) the dates of the photographs do coincide with the sampling, so here it could still be used to inform the discussion.

3.3.2. Collembola abundance

The RHS experimental plot Collembola abundance data did not fit the Poisson distribution, it was over-dispersed ($\mu = 22.6 \neq \sigma^2 = 872.4$). This is a commonly encountered problem in soil faunal data. For the Poisson distribution the mean should be approximately equal to the variance; the over-dispersion parameter theta should equal 1. Here an initial Poisson GLM was carried out which revealed a theta value of 20.7. This over-dispersion was mostly due to the wide range in Collembola abundances, however, the data also included ten sampling occasions where no Collembola were retrieved for a plot, as nine of these were from the RHS experimental plot dataset this contributed to the over-dispersion observed. Quasi-Poisson and negative binomial type models can handle over-dispersed count based data better: see Ver Hoef and Boveng (2007) for a comparison of these methods. Due to the degree of over-dispersion (theta >20), and the lower AIC values obtained, a negative binomial based starting model (link = log) was selected and carried out using the R package 'MASS' (Ripley et al. 2015).

For the Collembola dataset, during exploratory model building, the sample collected from H2ZB in October '12 was identified as having a high degree of influence; it was consistently found to be approaching Cook's distance. Models were built both including (Table 4., Figures 1. and 2., Appendix 3.4.2.) and excluding (Section 3.4.2.) this data point. Rationale for omission is given in the discussion (Section 3.5.1.1.). This removal meant that the design was no-longer balanced and as an interaction effect was found to be significant a Type III ANOVA was then performed to give significance levels for the remaining factors in the final model.

The Collembola densities across the RHS experimental plots and their adjacent grassland (for samples collected between October '11 and April '13) were also compared using a Kruskal-Wallis test; with the null hypothesis (H0): all Collembola densities belong to the same population and the alternative hypothesis (Ha): at least one of the Collembola site densities does not belong to the same population (the data were not normally distributed, Shapiro-Wilk: $p > 0.001$). Where H0 was rejected, the R package "dunn.test" (Dinno 2014) was used to run the Dunn post-hoc tests with a Bonferroni correction.

3.3.3. Acari abundance

The RHS experimental plot Acari abundance data contained no zeros, but was still over-dispersed and did not fit a Poisson distribution ($\mu = 91.6 \neq \sigma^2 = 7681.3$). Several starting models were a good fit for this data set, based on the AIC criterion a negative binomial model was selected (link = log).

The Acari densities across the RHS experimental plots and their adjacent grassland were also compared (for samples collected between October '11 and April '13) using a Kruskal-Wallis test; with the null hypothesis (H0): all Acari densities belong to the same population and the alternative hypothesis (Ha): at least one of the Acari site densities does not belong to the same population (the data were not normally distributed, Shapiro-Wilk: $p > 0.001$). Where H0 was rejected, the R package "dunn.test" (Dinno 2014) was used to run the Dunn post-hoc tests with a Bonferroni correction.

3.3.4. Species diversity analysis

In order for comparisons of species diversity (indices) between the plots to be valid the area sampled is required to be the same. Although the dry mass of the soil cores from

which the soil fauna were extracted was significantly different between sites (Kruskal-Wallis: χ^2 = 59.01, 5 d.f., $p < 0.001$) the volume of soil collected was the same for each sample (aside from for the adjacent grasslands where for April ’12, July ’12, October ’12 and April ’13 only one of the two soil cores were processed, see Section 3.2.2.. In the analysis pertaining solely to the RHS experimental plots the abundance and species richness can be directly compared between plots and treatments. When the other sites are compared, either densities have been used, as this takes account of the fact a smaller area has been sampled, or subsets of the data have been taken.

Absolute species richness (R) of each vegetation origin treatment (Native, Near native and Exotic) was calculated from all sampling occasions and plots combined, for each treatment at both the Deer’s Farm and Howard’s Field RHS experimental sites. Specimens mangled or unidentifiable to species/taxa grouping level were excluded from the diversity analysis. Where Buxton Wood and the heathland of Wisley Common were also considered, the July ’11 RHS experimental plot data was removed so that species richness could be compared for the same area and over the same length of time (equal sampling effort). Due to the sub-sampling of the adjacent grassland sites (see Section 3.2.2.) these diversity indices are not comparable. In Table 3.4.5.1. the number of soil cores the diversity metrics were derived from has been provided. See Table 1., Appendix 3.4.5., for an alternative analysis where one sample from each plot for each of the sampling occasions between April ’12 and April ’13 was randomly selected for comparison, so that each of the metrics is based on the same sampling effort over the same period of time (one sample from each of the following occasions: April ’12, July ’12, October ’12, April ’13). This subset is referred to again later.

When Collembola abundances at the species level were compared between the differing vegetation origin treatments, densities were used (Collembola kg-1) and as some of the abundances were low, the sampling occasions were pooled by season. Due to the data distributions a Kruskal-Wallis test was used with the null hypothesis (H0): all Collembola densities belong to the same population and the alternative hypothesis (Ha): at least one of the Collembola densities does not belong to the same population (is significantly greater or less than expected). Where H0 was rejected, the R package "dunn.test" (Dinno 2014) was used to run the Dunn post-hoc tests with a Bonferroni correction.

The R package "vegan" (Oksanen et al. 2013) was used to calculate Shannon-Weiner (H'), using natural logarithms, and Gini-Simpson (1-D) diversity indices (see Chapter 1., Section 1.5.2. for a description and Appendix 1.5.2. for the equations). As noted above for species richness, the data sets used included all occasion data for the RHS experimental plot analysis, but omitted July '11 when the other sites were considered. For the RHS experimental plots, two-way ANOVAs were performed in R for each of the sets of diversity indices after the data were found to be normally distributed (H' Shapiro-Wilk: p = 0.13 and 1-D Shapiro-Wilk: p = 0.4). **T**he null hypothesis (H0): all samples belong to the same population regarding treatment and the alternative hypothesis (Ha): at least one of the samples does not belong to the same population, with site and treatment as factors.

These diversity indices were also calculated for the subset of data from all sites, defined earlier in this section. One way ANOVAs were performed in R, for both H' and 1-D with site as the independent variable. The data for H' were not normally distributed (Shapiro-Wilk: p = 0.02), as the sample size was small, ANOVA was considered the most appropriate. The alternative non-parametric Kruskal-Wallis test was also performed and is

reported in the appendices. For 1-D the departure from normality was greater; again both ANOVA and the Kruskal-Wallis test were employed. The null hypothesis (H0): all samples belong to the same population and the alternative hypothesis (Ha): at least one of the samples does not belong to the same population. The post-hoc Tukey's HSD test was performed to explore instances where for an ANOVA factor $p < 0.05$ and the Dunn post-hoc tests (with a Bonferroni correction) where H0 was rejected following a significant Kruskal-Wallis result.

"Vegan" was also used to produce species accumulation curves (exact method), and conduct canonical correspondence analysis (CCA) on distinct taxonomic groups. For the multivariate analysis on the Collembola populations of the RHS experimental plots a CCA was performed to explore community-treatment relationships, using the data collected from all sampling occasions. Rare species were identified as those that only occurred in three or fewer samples and were excluded from further analysis. This was in an effort to reduce noise in the data set, this is a fairly arbitrary cut-off, but one that has previously been used within the literature in the comparison of Collembola communities (i.e. Shaw (2003)). Prior to this the species were log-transformed log(X + 1). For the genus *Entomobrya*, two species of which were included in the CCA, 36 Collembola were only identified to species level, as the highest abundances of these unidentified species were found in the same plots as the highest abundances of the identified species the identified species were still included in the analysis (Native: 20, Near native: 9, Exotic: 7 (pooled RHS experimental site)). Permutation tests were performed to determine significant factors in the ordinations (999 permutations).

For the multivariate analysis on the Collembola populations of all sites a CCA was performed to explore community-site relationships, the data from the July ’11 sampling occasion was omitted. As for the CCA on planting treatment; rare species were identified as those that only occurred in three or fewer samples and were excluded from further analysis. Prior to this the species were log-transformed log(X + 1). As above permutation tests were performed to determine significant factors in the ordinations (999 permutations).

3.4. Results

3.4.1. General results

A total of 11,824 Collembola and 41,756 Acari were collected over the duration of the study, from the 60 plots over the two RHS experimental sites: Deer’s Farm and Howard’s Field, their adjacent grassland and the less managed sites at Wisley Common and Buxton Wood. See Table 2. Appendix 3.4.2. for a full list of all Collembola species, with authorities, found and Table 3. Appendix 3.4.2. for the raw Collembola species and abundance data for each plot and sampling occasion.

Table 3.4.1.1. contains abundances of all major taxa found, for ease of viewing this has been summarised by Class or Order, expanded tables can be found in Appendix 3.4.1. Tables 1. and 2. for the Diplopoda and adult Coleoptera. Only one tardigrade (Phylum Tardigrada) was found (plot D6ZC April ’12). Symphyla, Pauropoda, Diplopoda and Chilopoda are Classes, though the latter two taxa were identified to Order (and species where possible for the Diplopoda). Within the Acariformes (Superorder), Acari were found from both the Sarcoptiformes (Astigmata and Oribatida) and the Trombidiformes (Prostigmata). The nematodes were grouped at the Phylum level Nematoda and the

Gastropods in the Class Gastropoda. The Haplotaxida (Order) includes the earthworm family: Lumbricidae and the potworm family: Enchytraeidae.

Table 3.4.1.1. Total abundances for major taxa groupings found under each site/treatment. N: Native, Z: Near native, E: Exotic, A: adjacent site, H: Wisley Common, W: Buxton Wood. As the adjacent sampling site for Deer's Farm was different between July'11 and other sampling occasions the Deer's Farm adjacent July'11 totals have been given in brackets after the overall total also including the Deer's Farm adjacent July '11 samples. For the holometabolous insects (Endopterygota) only the imagos have been included here.

	Deer's Farm				Howard's Field					
Taxa	**N**	**Z**	**E**	**A**	**N**	**Z**	**E**	**A**	**H**	**W**
Tardigrada	0	1	0	0	0	0	0	0	0	0
Isopoda	26	2	17	8 (8)	20	7	3	0	1	14
Chilopoda	1	3	4	16 (16)	8	4	0	2	27	28
Diplopoda	51	18	17	3 (2)	23	24	23	6	6	12
Pauropoda	61	67	60	9 (9)	49	30	27	2	0	39
Symphyla	8	2	1	0	2	2	0	3	26	0
Thysanoptera	2	1	0	29 (9)	2	2	1	69	15	14
Campodea	0	0	0	12 (12)	0	0	0	0	2	101
Protura	0	12	5	1 (0)	52	42	50	0	1	31
Collembola	908	618	584	1525 (338)	1185	1133	466	2249	1707	1451
Araneae	0	3	0	14 (3)	0	1	1	7	7	1
Pseudoscorpionida	0	0	0	0	0	0	0	0	1	0
Opiliones	1	0	0	0	0	0	0	0	0	0
Acariformes	2833	2114	1817	4858 (831)	5513	4353	3163	6792	7802	2511
Coleoptera	15	13	5	44 (9)	18	14	5	36	11	11
Psocoptera	3	0	1	1 (1)	1	0	0	1	0	0
Diptera	5	2	2	8 (1)	1	1	1	6	2	0
Hymenoptera	3	2	0	48 (1)	7	6	3	273	4	5
Hemiptera	6	4	11	29 (0)	9	5	12	45	6	0
Nematoda	2	0	0	15 (1)	4	3	5	24	3	0
Gastropoda	0	0	2	1 (1)	0	2	0	0	0	0
Haplotaxida	31	36	34	21 (9)	16	17	14	19	13	19

The Hymenoptera found include species in the family Formicidae (*Lasius niger* agg., *Myrmica* sp. *Stenamma* sp.) and members of the Parasitica (16 individuals, 3 of which were identified as belonging to the Family Ceraphronidae). Hemiptera families found

include: Aphididae, Rhopalidae, Lygaeidae, Tingidae, Anthocoridae and Cicadellidae. Some taxa are only transiently present in the soil at certain larval stages, this was seen for the Diptera where 387 larvae were found compared to 28 adults. For the Coleoptera 187 larvae were collected (mostly Elateridae from the woodland) and 172 adults across all sites/treatments.

For the Chilopoda many of the individuals were juveniles where it was not possible to identify them to the species level, however, *Scutigera coleoptrata* (house centipede) was easily recognised as it is the only British Scutigeramorpha species (Barber 2008), see Table 3.4.1.2. for the distribution of the centipede Orders.

Table 3.4.1.2. Total abundances for the Chilopoda, separated into Orders found under each site/treatment. N: Native, Z: Near native, E: Exotic, A: adjacent site, H: Wisley Common, W: Buxton Wood. As the adjacent sampling site for Deer's Farm was different between July'11 and other sampling occasions, the Deer's Farm adjacent July '11 totals have been given in brackets after the overall total also including the Deer's Farm adjacent July '11 samples.

	Deer's Farm				Howard's Field					
Chilopoda (Order)	**N**	**Z**	**E**	**A**	**N**	**Z**	**E**	**A**	**H**	**W**
Geophilomorpha	1	3	0	5 (5)	4	0	0	1	23	27
Lithobiomorpha	0	0	4	11 (11)	3	4	0	0	0	1
Scolopendromorpha (*Cryptops* sp.)	0	0	0	0	1	0	0	0	0	4
Scutigeramorpha (*Scutigera coleoptrata)*	0	0	0	0	0	0	0	1	0	0

When examining Tables 3.4.1.1. and 3.4.1.2. it is important to remember that no samples were collected from Wisley Common or Buxton Wood in July' 11 so those totals come from a smaller volume of soil and that for the April '12, July '12, October '12 and April '13 sampling occasions only one of the two samples collected was processed for the adjacent sites (see Section 3.2.2. of this chapter).

3.4.2. Collembola abundance

There was no significant difference in the dry soil mass of the cores the Collembola were extracted from between the different vegetation origin treatments of the RHS experimental plots (Kruskal-Wallis: χ^2 =3.8, 2 d.f., p = 0.149) and so converting to density of Collembola kg-1 did not change the relationship between the treatments, see Figure 3.4.2.1. The mean densities of Collembola found at each site/treatment are shown in Table 3.4.2.1..

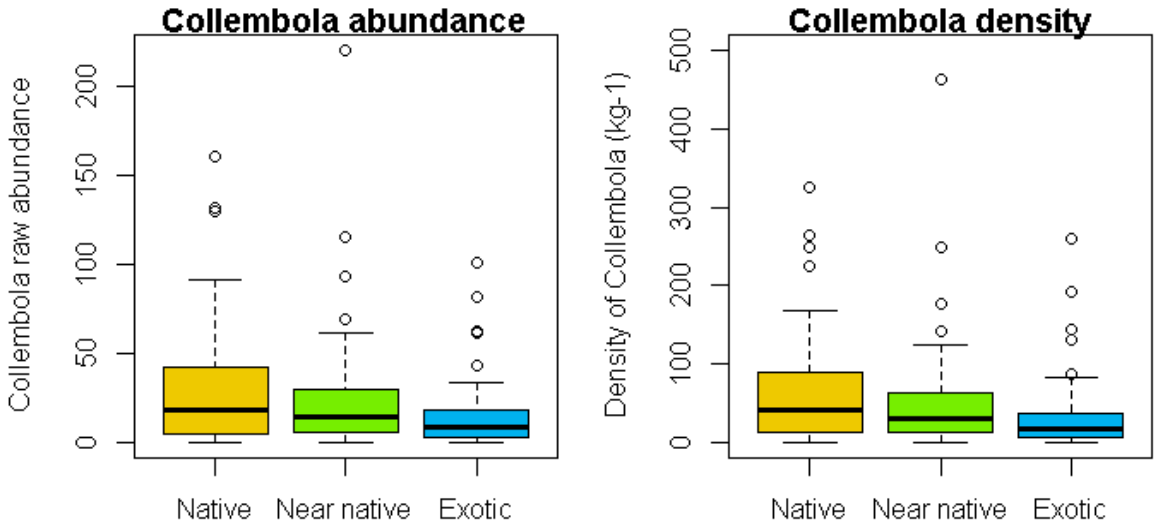

Figure 3.4.2.1. Left: Boxplots of the total Collembola abundance recorded for both the Deer's Farm and Howard's Field RHS experimental plots for all occasions under each of the planting treatments: Native (yellow), Near native (green) and Exotic (blue). **Right**: Boxplots of the density of Collembola (kg-1) recorded for both the Deer's Farm and Howard's Field sites for all occasions under each of the planting treatments: Native (yellow), Near native (green) and Exotic (blue).

Table 3.4.2.1. Mean Collembola density (Collembola per kg of soil sampled) for each of the treatments and sampling occasions.

		Mean density of Collembola (kg-1)					
Site	**Treatment**	**July '11**	**Oct '11**	**Apr '12**	**July '12**	**Oct '12**	**Apr '13**
Deer's Farm	**Native**	20.34	17.09	71.94	106.33	44.90	93.64
	Near native	1.47	11.60	40.72	61.38	33.57	71.34
	Exotic	11.06	24.54	45.98	18.65	36.88	76.12
	Adjacent	99.90	49.32	250.09	158.19	140.44	63.48
Howard's Field	**Native**	16.82	5.80	124.33	110.91	44.38	92.09
	Near native	31.66	12.80	26.29	132.23	106.39	76.63
	Exotic	16.71	8.55	28.90	39.33	17.45	44.68
	Adjacent	110.24	175.41	131.76	232.17	186.54	232.78
Wisley Common		NA	32.54	257.56	107.99	97.08	289.21
Buxton Wood		NA	83.20	127.46	43.41	164.82	273.15

A GLM based on the Collembola data (without the H2ZB point) found that abundance was significantly associated with soil moisture, season, vegetation origin treatment and the interaction between soil moisture and season, see Table 3.4.2.2.. In the GLM neither RHS experimental site, nor pH, nor planting mix were found to significantly affect Collembola abundance, all these terms were removed during the stepwise deletion of non-significant terms. See Figure 3., Appendix 3.4.2., for the plots of the residuals from the initial global model and Figure 4., for the plots of the residuals from the final model. See Figure 3.4.2.2. for the mean Collembola densities across both the RHS experimental sites for all treatments and seasons (spring: July '11 and '12, autumn: Oct '11 and Oct '12, spring: April '12 and April '13).

Table 3.4.2.2. Type III analysis of variance table for the significant terms in RHS experimental plot Collembola abundance model excluding the sample collected in October '12 from H2ZB. Final model: Adjusted R^2 = 0.9917, AIC = 1702.4.

Term	d.f.	F value	p value	
Soil moisture	1	28.14	p = 2.9 e-7	***
Season	2	11.25	p = 2.3 e-5	***
Soil moisture : Season (interaction)	2	8.16	p = 0.0004	***
Vegetation origin treatment	2	5.86	p = 0.003	**

*: p < 0.05, **: p < 0.01, ***: p < 0.001

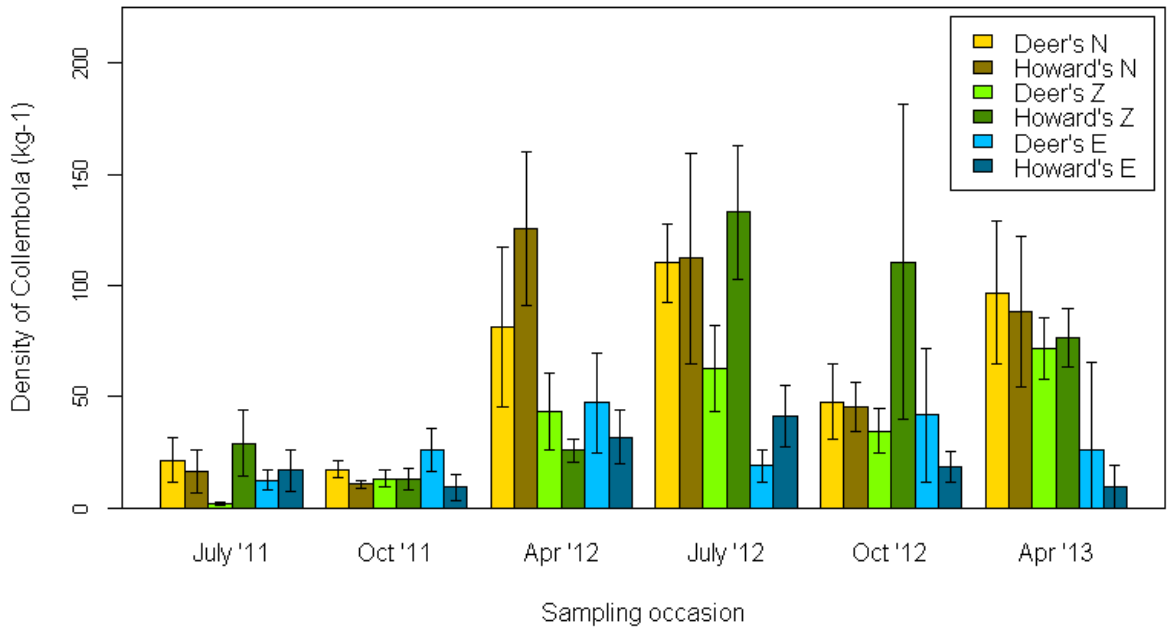

Figure 3.4.2.2. Barchart of the mean density of Collembola (kg-1) for all treatments and all sampling occasions for both the RHS experimental plots at the Deer's Farm site (lighter left hand tones) and the Howard's Field site (darker right hand tones). Native (N) bars (yellow), Near native (Z) bars (green) and Exotic (E) bars (blue). Error bars plotted using the standard error.

The Collembola abundance model using the entire data set can be found in Appendix 3.4.2., Table 4., however, this includes a sample (collected in October '12 from H2ZB) that is approaching Cook's distance in the initial global starting model (see Figure 1., Appendix 3.4.2.) and once the stepwise deletion of non-significant terms was approximately 0.5 and was considered likely to be having undue leverage on the resulting model (see Figure 2., Appendix 3.4.2.), a rationale for its removal is given in Section 3.5.1.1..

Collembola densities were significantly greater for the adjacent grassland, see Figure 3.4.2.3. for the densities separated by season. A Kruskal-Wallis test revealed a significant difference in Collembola density across the RHS experimental sites and their adjacent grassland ($\chi^2 = 52.4$, 3 d.f., $p < 0.001$), H0 was rejected.

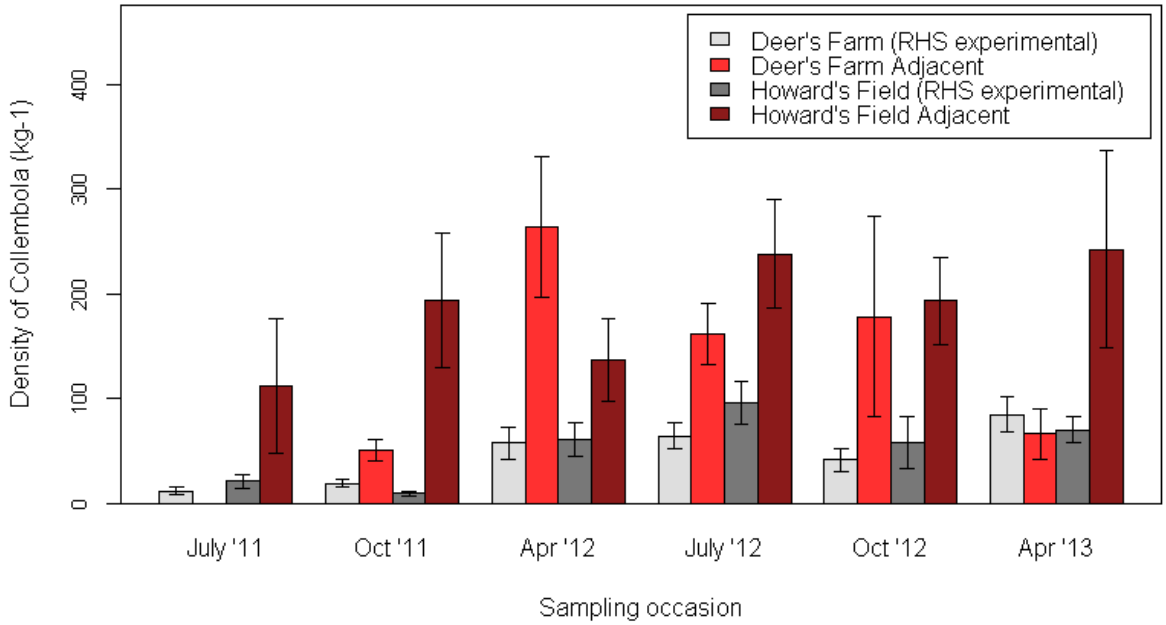

Figure 3.4.2.3. Barchart of the mean density of Collembola (kg-1) for the RHS experimental plots and their adjacent grassland. Deer's Farm RHS experimental plots: light grey, Howard's Field RHS experimental plots: dark grey, Deer's Farm adjacent plots: light red, Howard's Field adjacent plots: dark red. Error bars plotted using the standard error. Deer's Farm adjacent first sampling occasion not included.

A post-hoc Dunn test showed that the significant differences lay between the RHS experimental sites and the grassland sites, see Figure 3.4.2.4.. There was a significant difference between the Deer's Farm RHS experimental plots and both the adjacent grassland sites (DFA: $Z = 3.88$, $p < 0.001$, HFA: $Z = -6.12$, $p < 0.001$) and the Howards Field RHS experimental plots and both the adjacent grassland sites (DFA: $Z = 3.79$, $p < 0.001$, HFA: $Z = 6.02$, $p < 0.001$): the adjacent grasslands have higher densities of Collembola

than the RHS experimental plots. There was no significant difference between the two RHS experimental sites ($Z = -0.14$, $p > 0.05$) or the two adjacent grassland sites ($Z = -1.83$, $p > 0.05$). Figure 3.4.2.5. shows the variation in Collembola densities across all the sites sampled for the duration of the study.

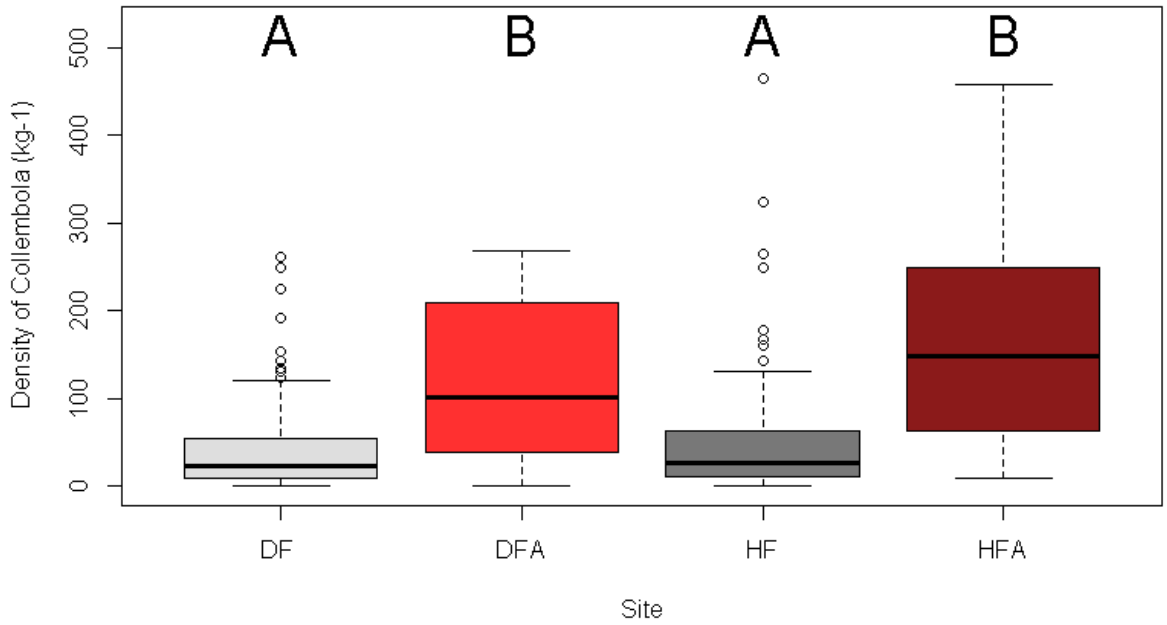

Figure 3.4.2.4. Boxplots of the mean densities of Collembola (kg-1) for the RHS experimental plots and their adjacent grassland. DF: Deer's Farm RHS experimental plots: light grey, DFA: Deer's Farm adjacent plots: light red, HF: Howard's Field RHS experimental plots: dark grey, HFA: Howard's Field adjacent plots: dark red. Sites underneath the same letter do not differ according to the Dunn's post-hoc test.

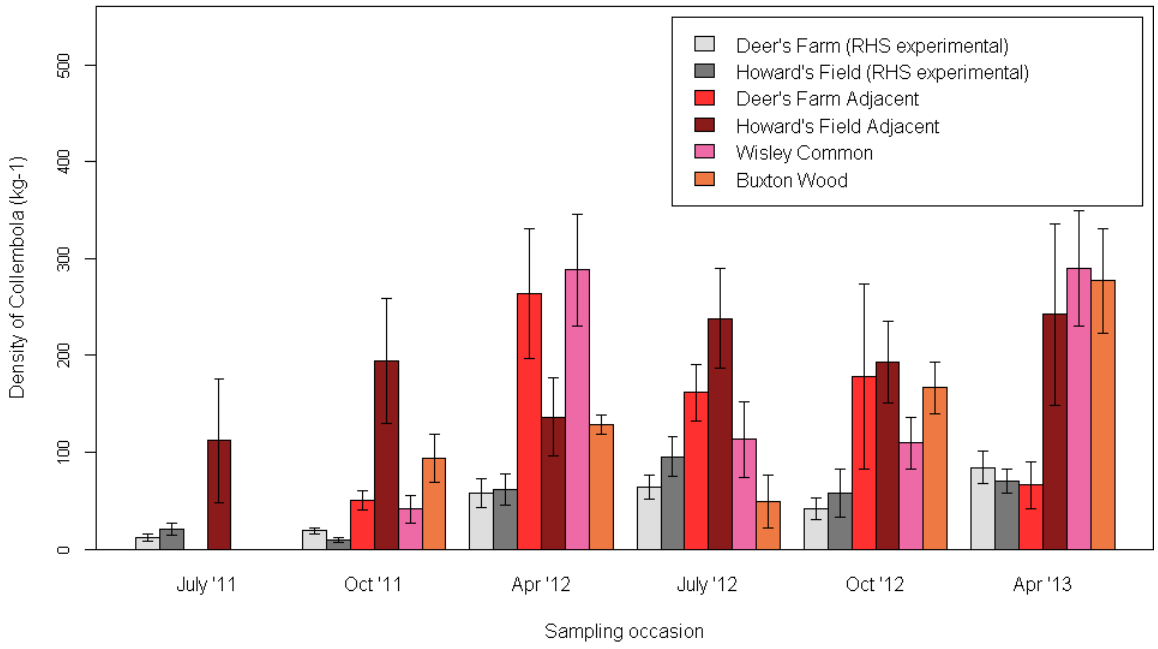

Figure 3.4.2.5. Barchart of the mean density of Collembola (kg-1) for the RHS experimental plots, their adjacent grassland, Wisley Common and Buxton Wood. Deer's Farm RHS experimental plots: light grey, Howard's Field RHS experimental plots: dark grey, Deer's Farm adjacent plots: light red, Howard's Field adjacent plots: dark red, Wisley Common: pink, Buxton Wood brown. Error bars plotted using the standard error.

3.4.3. Acari abundance

The mean densities of Acari under each site/treatment are given in Table 3.4.3.1., as with the Collembola converting to density of Acari kg-1 did not change the relationship between the treatments, see Figure 3.4.3.1..

Table 3.4.3.1. Mean Acari density (Acari per kg of soil sampled) for each of the treatments and sampling occasions.

		Mean density of Acari (kg-1)					
Site	**Treatment**	**July '11**	**Oct '11**	**Apr '12**	**July '12**	**Oct '12**	**Apr '13**
Deer's Farm	**Native**	115.74	284.97	130.69	234.89	199.18	222.71
	Near native	16.13	152.70	82.17	179.11	147.15	202.98
	Exotic	47.92	151.33	134.56	61.49	93.35	201.59
	Adjacent	245.61	448.23	522.56	284.26	158.00	563.25
Howard's	**Native**	252.61	290.13	143.66	479.32	449.10	284.30
Field	**Near native**	249.05	150.18	116.13	497.42	223.58	281.08
	Exotic	142.92	107.68	156.58	252.37	109.30	289.54
	Adjacent	370.43	573.28	727.84	297.13	490.43	743.11
Wisley Common		NA	301.38	1051.27	464.09	729.22	922.49
Buxton Wood		NA	243.43	132.75	72.73	256.76	506.82

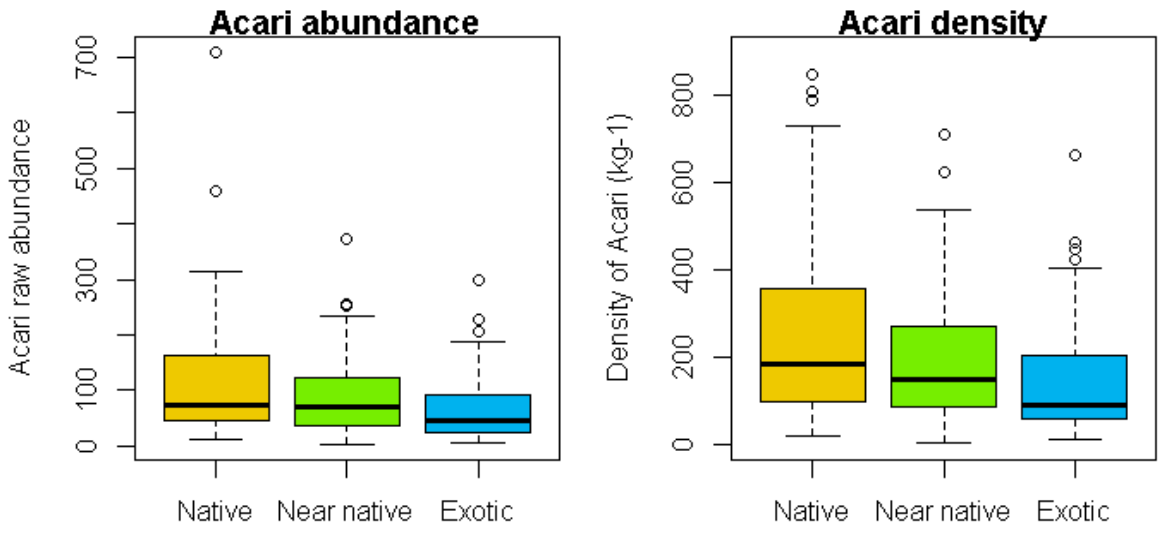

Figure 3.4.3.1. Left: Boxplots of the total Acari abundance recorded for both the Deer's Farm and Howard's Field RHS experimental sites for all occasions under each of the planting treatments: Native (yellow), Near native (green) and Exotic (blue). **Right**: Boxplots of the density of Acari (kg-1) recorded for both the Deer's Farm and Howard's Field RHS experimental sites for all occasions under each of the planting treatments: Native (yellow), Near native (green) and Exotic (blue).

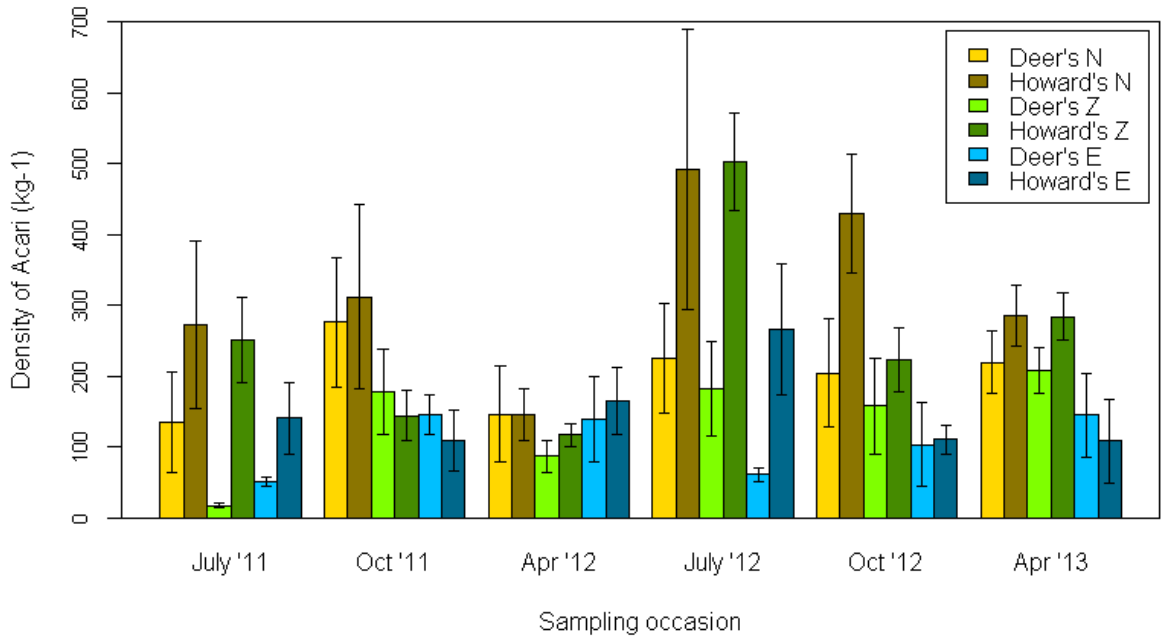

Figure 3.4.3.2. Barchart of the mean density of Acari (kg-1) for all treatments and all sampling occasions for both the RHS experimental plots at the Deer's Farm site (lighter left hand tones) and the Howard's Field site (darker right hand tones). Native (N) bars (yellow), Near native (Z) bars (green) and Exotic (E) bars (blue). Error bars plotted using the standard error.

A GLM based on the Acari data found that abundance was significantly associated with pH, vegetation origin and season, and the interaction between vegetation origin and season, see Table 3.4.3.2.. Neither RHS experimental site nor planting mix were found to significantly affect Acari abundance, these factors were removed during the stepwise deletion of non-significant terms. See Figure 1., Appendix 3.4.3., for the plots of the residuals from the initial global model, Figure 2. for the residuals prior to the final stepwise deletion of the non-significant term: soil moisture (P = 0.1) and Figure 3., for the plots of the residuals from the final model. See Figure 3.4.3.2. above for the mean Acari densities across both the RHS experimental sites for all treatments and seasons (spring: July '11 and '12, autumn: Oct '11 and Oct '12, spring: April '12 and April '13).

Table 3.4.3.2. Type III analysis of variance table for the significant terms in RHS experimental plot Acari abundance final model. Final model: Adjusted R^2 = 0.9996, AIC = 2336.

Term	d.f.	F value	p value	
pH	1	32.98	p = 3.3 e-8	***
Vegetation origin treatment	2	6.42	p = 0.002	**
Season	2	5.27	p = 0.006	**
Vegetation origin treatment : Season (interaction)	4	2.56	p = 0.04	*

*: p < 0.05, **: p < 0.01, ***: p < 0.001

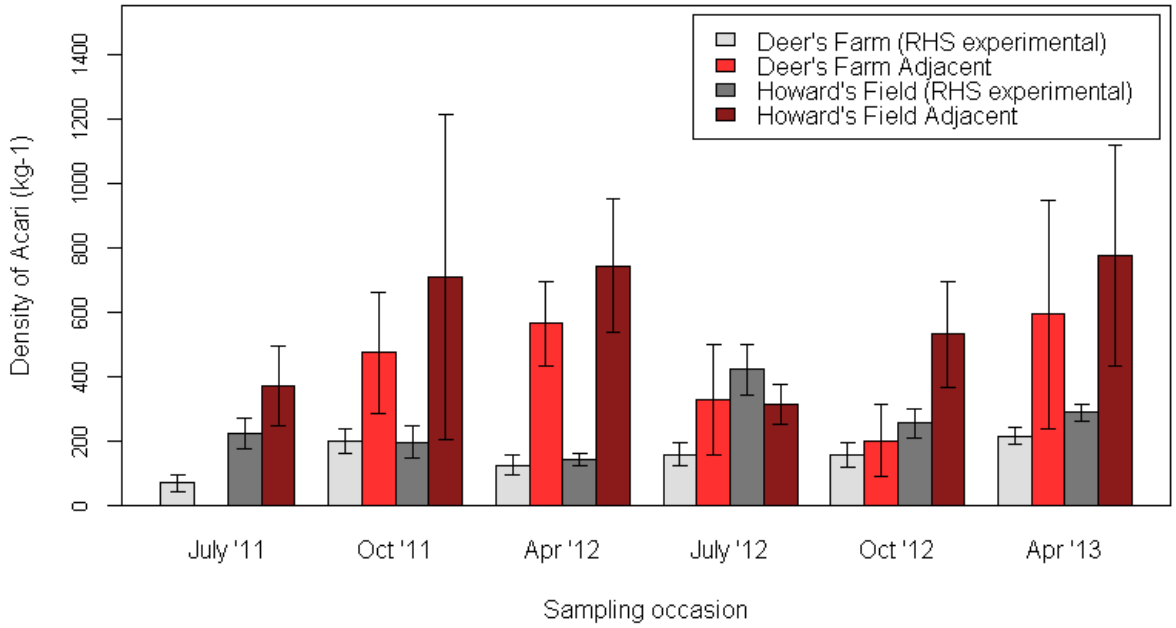

Figure 3.4.3.3. Barchart of the mean density of Acari (kg-1) for the RHS experimental plots and their adjacent grassland. Deer's Farm RHS experimental plots: light grey, Howard's Field RHS experimental plots: dark grey, Deer's Farm adjacent plots: light red, Howard's Field adjacent plots: dark red. Error bars plotted using the standard error. Deer's Farm adjacent first sampling occasion not included.

Acari densities differed across the RHS experimental sites and the adjacent grassland, see Figure 3.4.3.3., a Kruskal-Wallis test revealed a significant difference in Acari density across the RHS experimental sites and their adjacent grassland (χ^2 = 31.3, 3 d.f., p < 0.001), H0 was rejected. A post-hoc Dunn test showed that the significant differences lay between the Deer's Farm RHS experimental site which had significantly lower densities of Acari than all the other sites and between the Howard's Field RHS experimental site and its adjacent grassland, see Table 3.4.3.3. for the relevant statistics. Figure 3.4.3.4. shows the variation in Acari densities across all the sites sampled for the duration of the study.

Table 3.4.3.3. Dunn's post-hoc test results: Z statistics and p values for multiple comparisons of Acari density between sites. *'s denote results were there was a significant difference.

	Deer's Farm	**Howard's Adjacent**	**Deer's Adjacent**
Howard's Adjacent	**Z = -5.28** **p < 0.001 *** **		
Deer's Adjacent	**Z = 2.84** **p < 0.05 * **	**Z = -2.00** **NS**	
Howard's Field	**Z = -3.15** **p < 0.01 ** **	**Z = -2.83** **p < 0.05 * **	**Z = 0.61** **NS**

NS: p > 0.05

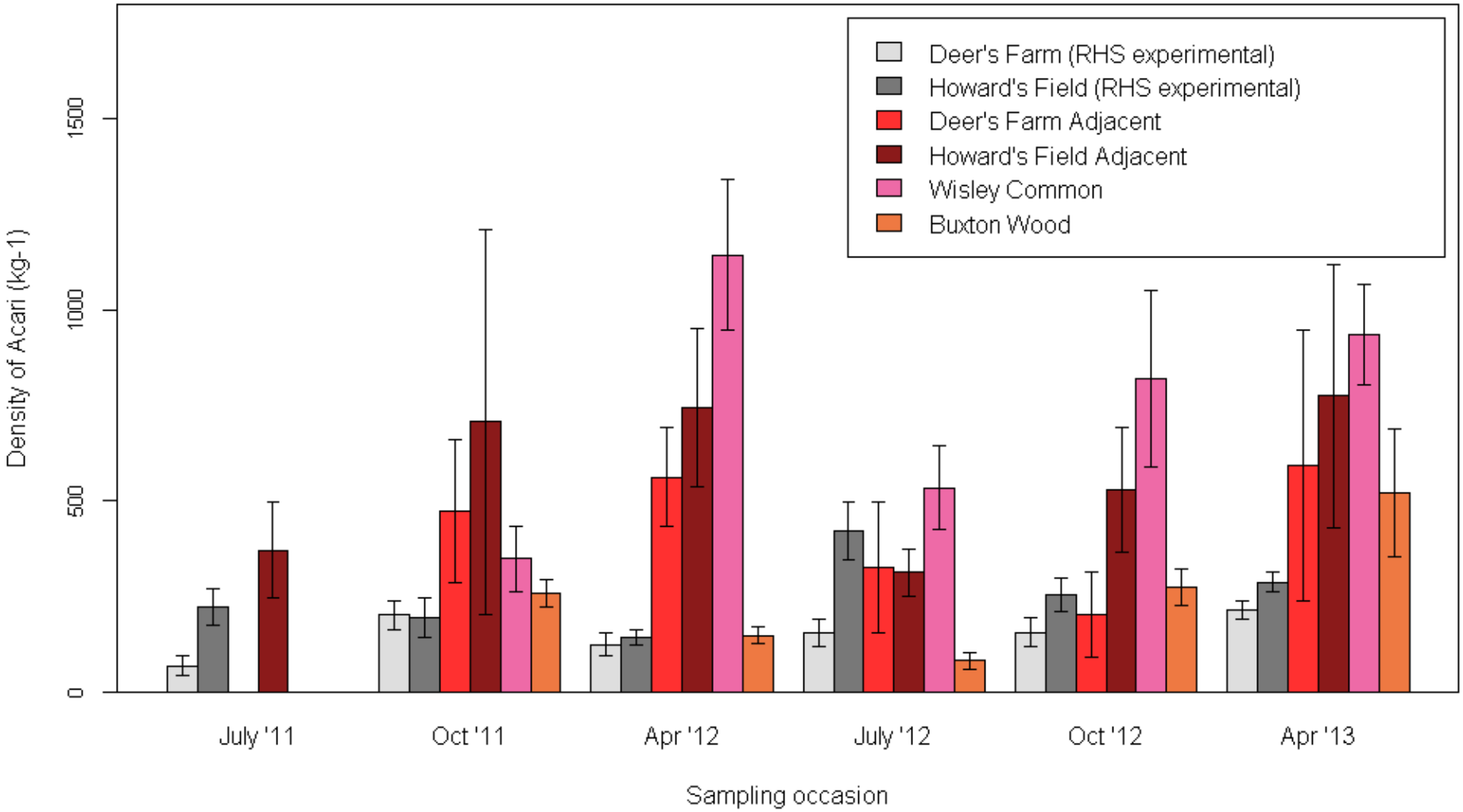

Figure 3.4.3.4. Barchart of the mean density of Acari (kg-1) for the RHS experimental plots, their adjacent grassland, Wisley Common and Buxton Wood. Deer's Farm RHS experimental plots: light grey, Howard's Field RHS experimental plots: dark grey, Deer's Farm adjacent plots: light red, Howard's Field adjacent plots: dark red, Wisley Common: pink, Buxton Wood brown. Error bars plotted using the standard error.

3.4.4. Collembola diversity: RHS experimental plots

A total of 69 Collembola species were found in this study (Table 3. Appendix 3.4.2.) although several of these species were grouped at the genus level, see Section 3.2.2. of this chapter. In total 44 species/species groupings were retrieved from the RHS experimental plots, not all of these taxa were found at both of the study sites: 31 species and 36 species were found at Deer's Farm and at Howard's Field respectively. See Figure 3.4.4.1. for species accumulation curves for both of the RHS experimental sites and Figure 3.4.4.2. for the plots separated by vegetation origin treatment. For all treatments total species richness was greater at the Howard's Field experimental plots than at Deer's Farm, see Table 3.4.4.1..

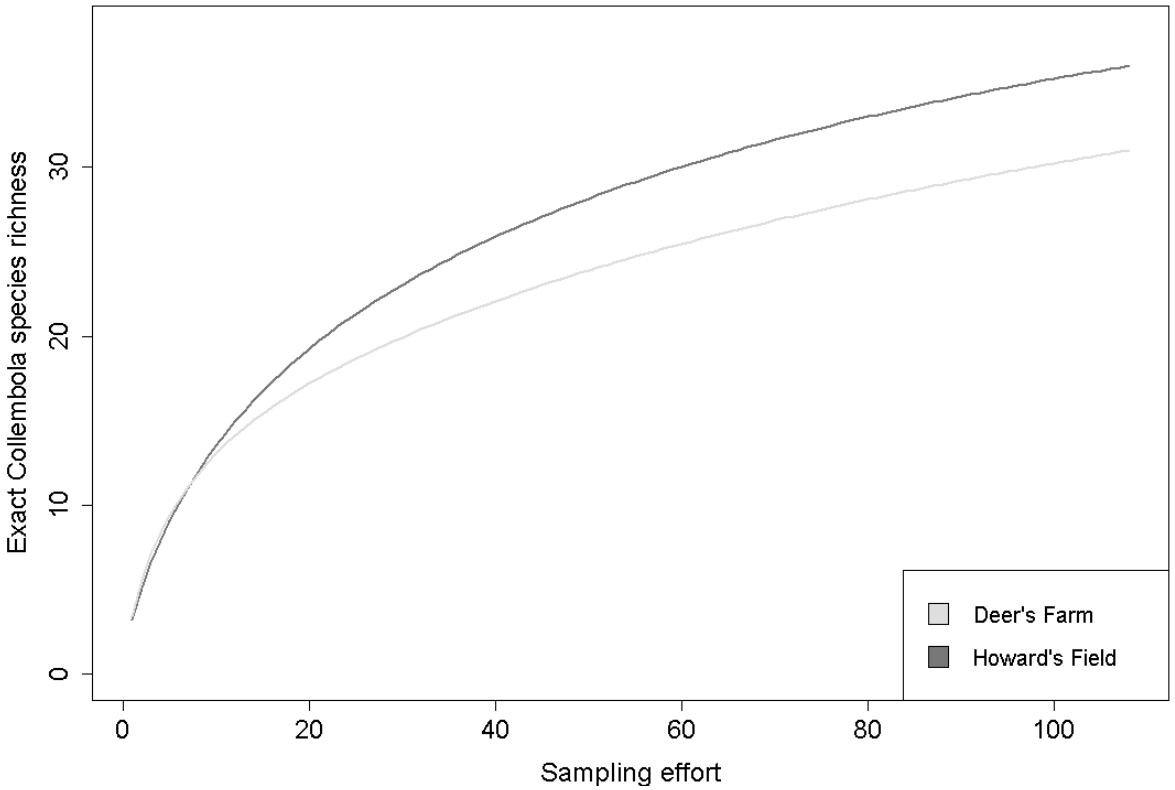

Figure 3.4.4.1. RHS experimental plots species accumulation curves for the two RHS sites: Deer's Farm (light grey) and Howard's Field (dark grey). One unit of sampling effort is one sampling occasion for one plot.

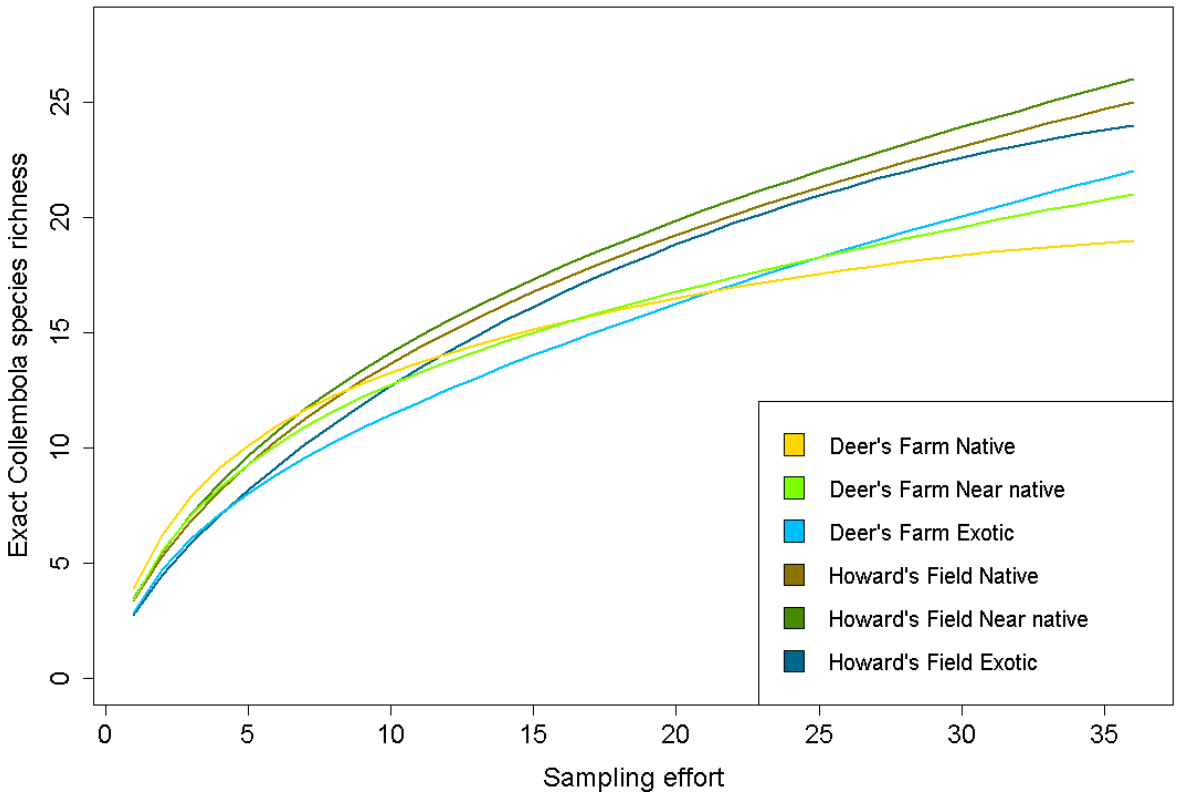

Figure 3.4.4.2. RHS experimental plots species accumulation curves for all treatments (Native; yellow, Near native; green and Exotic; blue) at both Deer's Farm (lighter tones) and Howard's Field (darker tones). One unit of sampling effort is one sampling occasion for one plot.

Table 3.4.4.1. Metrics of species diversity: Species richness (R), Shannon-Weiner (H') (natural logarithms) and Gini-Simpson (1-D) for the RHS experimental plots: absolute species richness was calculated per treatment and species diversity indices per plot (pooled sampling occasion).

Site	Treatment	R	H'	1-D
Deer's Farm	**Native**	19	1.33 ± 0.16	0.58 ± 0.06
	Near native	21	1.33 ± 0.10	0.61 ± 0.04
	Exotic	22	1.39 ± 0.14	0.65 ± 0.06
Howard's Field	**Native**	25	1.05 ± 0.11	0.50 ± 0.04
	Near native	26	0.98 ± 0.09	0.44 ± 0.05
	Exotic	24	1.25 ± 0.16	0.56 ± 0.06

From the RHS experimental plots 2 specimens were considered too mangled for any identification and 62 unidentifiable to the required taxon level (e.g. this included 36 *Entomobrya* sp. where there was sufficient damage to the dorsal side of the abdominal segments to prevent further identification as separation is based on pigmentation patterning in this region) see Table 1. Appendix 3.4.4. for abundances and location of specimens excluded from analysis.

A CCA testing whether the abundances of the 20 most common Collembola differed between the two RHS experimental sites found that site was a significant factor (permutation test: F = 3.0728, 1 d.f., p = 0.001) see Figure 3.4.4.3. for an enlarged figure of the centre of the ordination plot and Appendix 3.4.4., Figure 1. for the full graphical representation. See Table 6. Appendix 3.4.4. for the species included.

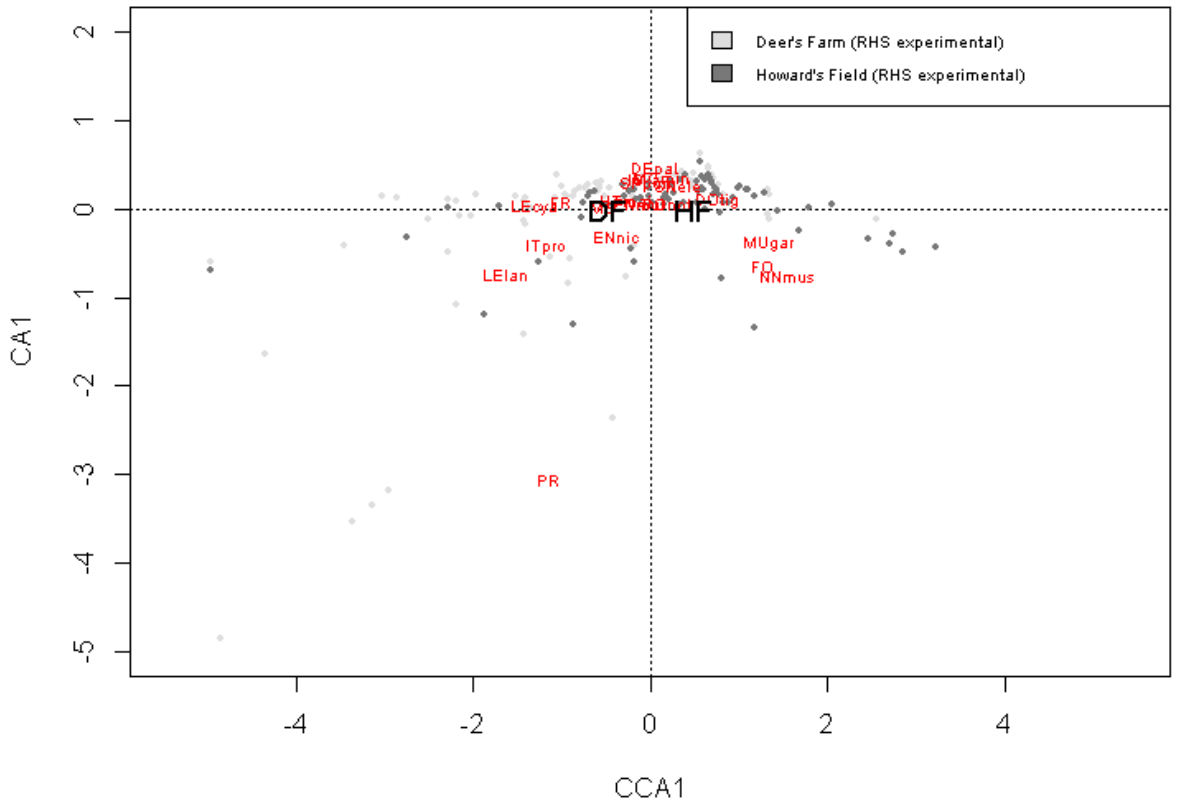

Figure 3.4.4.3. CCA ordination diagram of RHS experimental plot main Collembola species abundances (log-transformed) separated by site. Black labels represent site centroids: DF: Deer's Farm and HF: Howard's Field. Red labels are Collembola species codes, see Appendix 3.4.2., Table 2., for interpretation and Appendix 3.4.4., Figure 1. for full ordination diagram.

A CCA testing whether the abundances of the most common Collembola differed between vegetation origin treatment found that treatment was a significant factor (permutation test: F = 1.8516, 2 d.f., p = 0.005) see Figure 3.4.4.4. for an enlarged figure of the centre of the ordination plot and Appendix 3.4.4., Figure 2. for the full graphical representation. See Table 6. Appendix 3.4.4. for the species included.

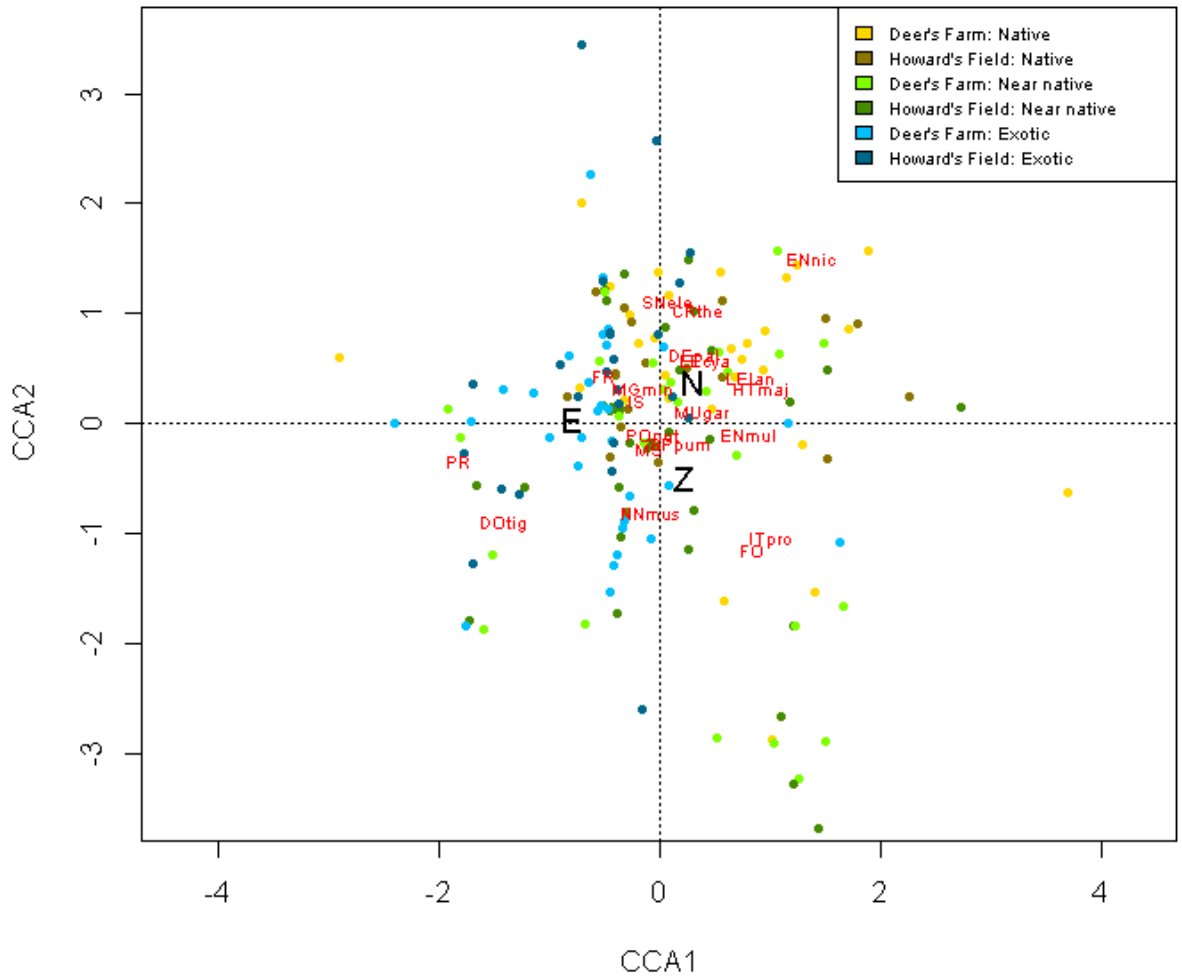

Figure 3.4.4.4. CCA ordination diagram of RHS experimental plot main Collembola species abundances (log-transformed) separated by vegetation treatment. Black labels represent treatment centroids: N: Native, Z: Near native and E: Exotic. Red labels are Collembola species codes, see Appendix 3.4.2., Table 2. for interpretation and Appendix 3.4.4. Figure 2. for full ordination diagram.

Across all treatments and sites the most common species was *Parisotoma notabilis* accounting for 30% of all Collembola retrieved and when only the RHS experimental plots were considered this increased to 58%. Kruskal-Wallis tests revealed significant differences in species distribution under the differing vegetation origin treatments for three of the species found at the RHS experimental plots: *P. notabilis*, *Cryptopygus thermophilus* and *Sphaeridia pumilis*, see Table 3.4.4.2. for a summary of these results and Tables 2., 3. and 4. Appendix 3.4.4. for full results for summer (July '11 and July '12), autumn (October '11 and October '12) and spring (April '12 and April '13), respectively.

Table 3.4.4.2. Summary data for Collembola mean density (kg-1) per plot ± standard error for both RHS experimental sites separated by season, where significant differences between treatment effects were found by the Kruskal-Wallis test. N: Native, Z: Near native, E: Exotic. Non-shaded region: summer, shaded region: autumn. See Table 2. Appendix 3.4.2. for interpretation of species codes and Tables 2.-4. Appendix 3.4.4. for full results.

	Deer's Farm			Howard's Field			Treatment
Taxa	N	Z	E	N	Z	E	effect
POnot	45.56 ± 11.13	21.47 ± 6.97	6.66 ± 3.06	46.22 ± 19.59	69.43 ± 13.87	21.69 ± 7.5	*
HTmaj	2.32 ± 0.42	1.14 ± 0.6	0.18 ± 0.18	2.66 ± 1.45	2.05 ± 1.14	0.51 ± 0.36	*
HTmaj	3.24 ± 1.4	-	-	0.15 ± 0.15	-	-	**
SPpum	-	-	-	-	0.7 ± 0.35	-	*

-: Not recorded, *: $p < 0.05$, **: $p < 0.01$

Within the RHS experimental plots other species of note found include: *Willemia intermedia* (plot: H2ZB (July '12 and October '12)) the non-native species *Katianna schoetti* (see Figure 3.4.4.5.) and another alien Symphypleona species provisionally called '*Katianna* species 4' (Ardron 2009; Janssens 2014) (see Figure 3.4.4.6.).

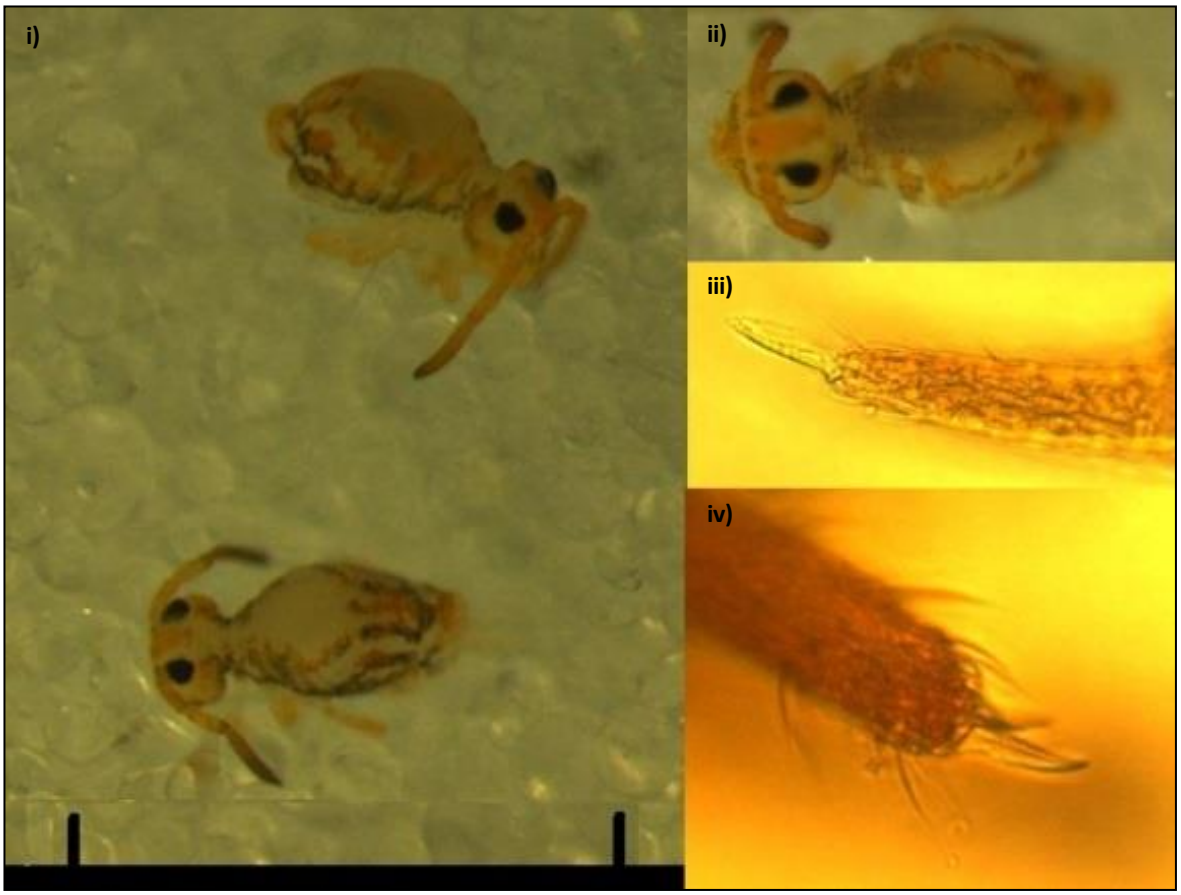

Figure 3.4.4.5. Images of *Katianna schoetti* retrieved from the RHS experimental plots in April '13. i) *K. schoetti* from the Exotic treatment at Howard's Field (plot H1EA), scale in mm. ii) *K. schoetti* from the Near native treatment at Howard's Field (plot H4ZC). iii) mucro and furca of Collembola in image ii). iv) claw of Collembola in ii).

In total eight exotic Katiannids were retrieved, all from Howard's Field, accounting for 0.2% of the total Collembola abundance at that site (plots: H5EB (October '12) and plots H5EB, H6EA and H6ZA (April '13)). For '*Katianna* sp. 4' between treatment differences in species density were not statistically significant for autumn (K-W test: χ^2 = 2, 2.d.f., p > 0.05) or spring (K-W test: χ^2 = 2, d.f. p > 0.05). The same was true for *K. schoetti* which was only recorded in the spring (K-W: χ^2 = 2.2, 2.d.f., p > 0.05).

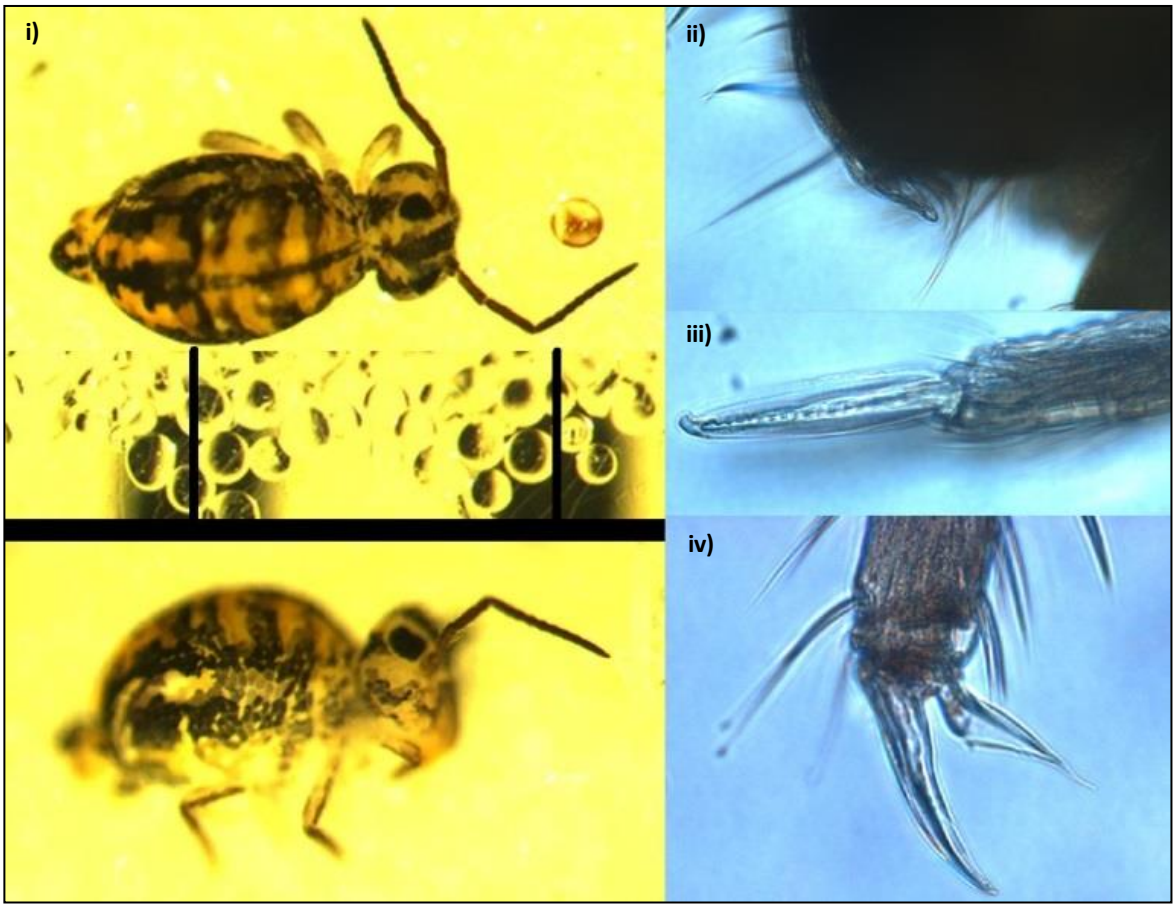

Figure 3.4.4.6. Images of an alien *Katianna* sp. retrieved from the Exotic RHS experimental plot treatment at Howard's Field in Oct '12 (plot H1EA). i) dorsal and lateral pigmentation, scale in mm. ii) female subanal appendage. iii) mucro. iv) foot complex of third leg.

A two-way ANOVA test revealed a significant difference in H' between the Deer's Farm and Howard's Field RHS experimental sites ($F_{1, 30}$ = 6.045, p < 0.05). No significant difference in treatment was found between the vegetation origin treatments ($F_{2, 30}$ = 0.905, p > 0.05), H0 was accepted, see Figure 3.4.4.7. for a graphical representation of the H' diversity indices of the RHS experimental sites separated by plot treatment. See

Appendix 3.4.4., Table 5. and Figure 3. for the full two-way ANOVA results including interaction terms and the plots of the residuals, respectively.

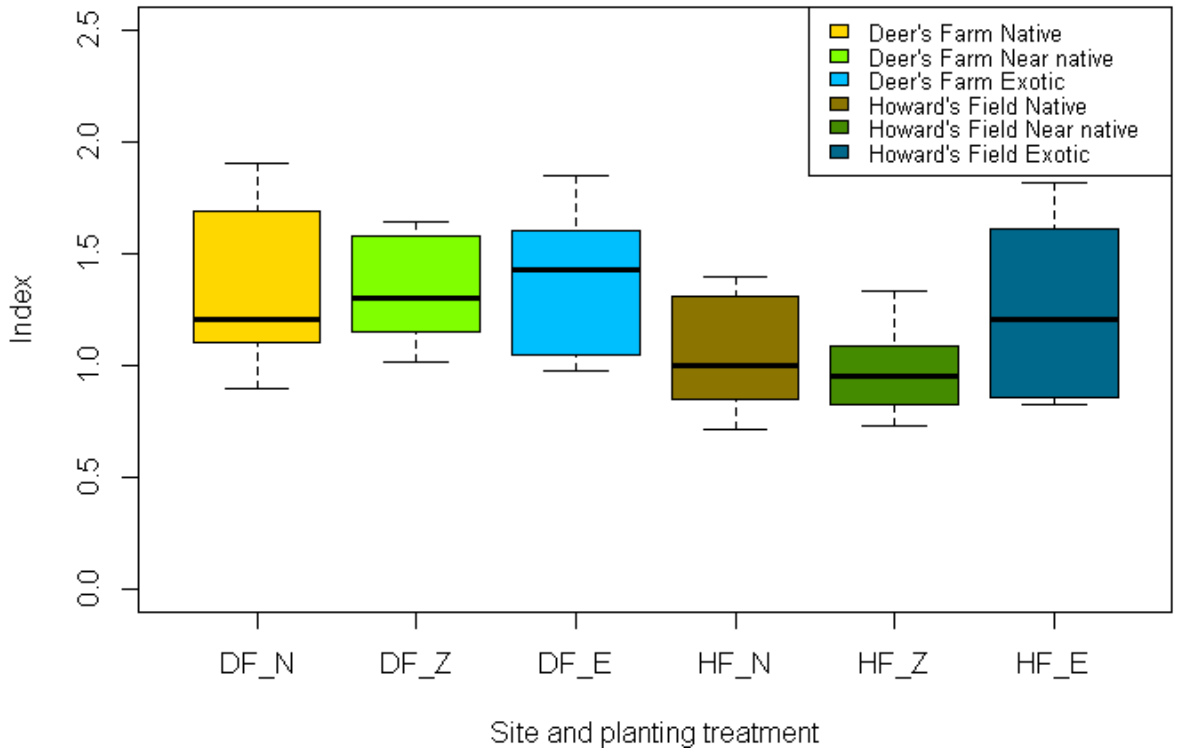

Figure 3.4.4.7. Shannon-Weiner diversity indices for the RHS experimental plots at the Deer's Farm site (DF: lighter left hand tones) and the Howard's Field site (HF: darker right hand tones). Native (N): yellow, Near native (Z): green, and Exotic (E): blue.

A two-way ANOVA test also revealed a significant difference in 1-D between the RHS experimental sites ($F_{1, 30} = 6.751$, $p < 0.05$). Again no significant difference in treatment was found between the vegetation origin treatments ($F_{2, 30} = 1.431$, $p > 0.05$), H0 was accepted, see Figure 3.4.4.8. for a graphical representation of the 1-D diversity indices of the RHS experimental sites separated by plot treatment. See Appendix 3.4.4., Table 5. and Appendix 3.4.4., Figure 4. for the full two-way ANOVA results including interaction terms and the plots of the residuals, respectively.

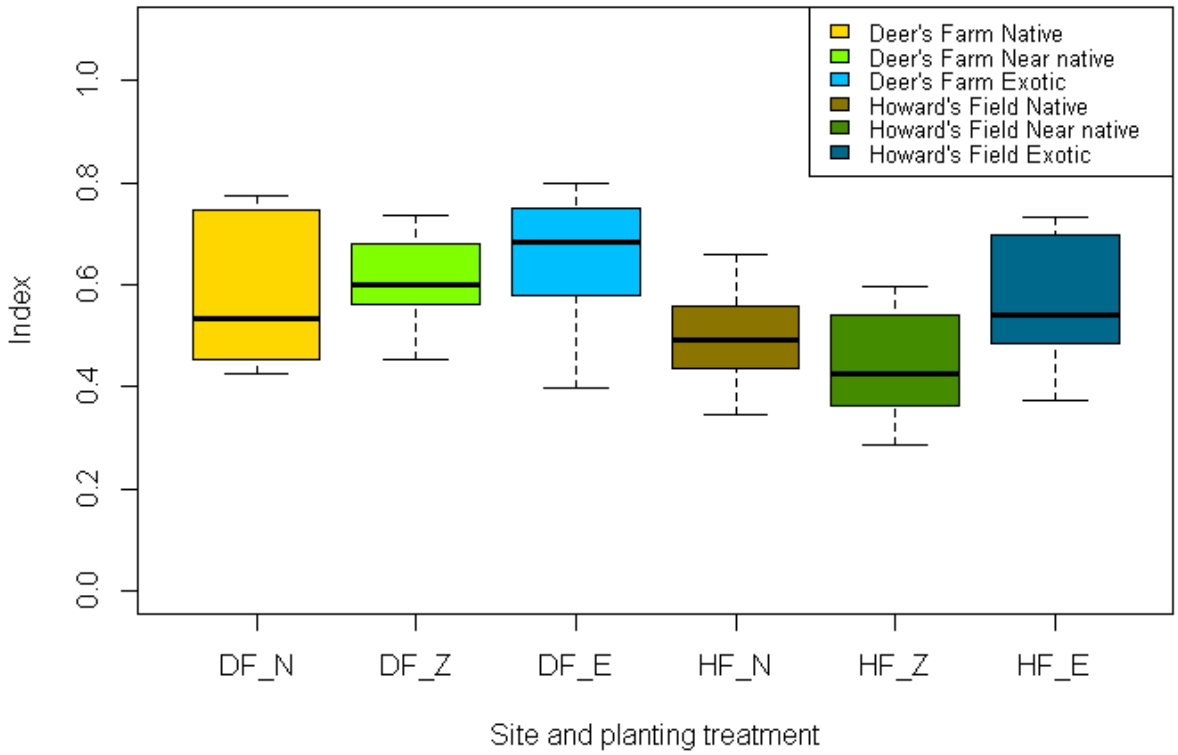

Figure 3.4.4.8. Gini-Simpson diversity indices for the RHS experimental plots at the Deer's Farm site (DF: lighter left hand tones) and the Howard's Field site (HF: darker right hand tones). Native (N): yellow, Near native (Z): green, and Exotic (E): blue.

3.4.5. Collembola diversity: All sites

Across all sites 65 Collembola taxa groupings (69 species) were found. Two species*:* *Parisotoma notabilis* and *Sminthurinus aureus*, and three taxa groupings *Isotoma* spp. (*I. anglicana* and *I. viridis*), *Friesea* spp. (*F. claviseta*, *F. mirabilis* and *F. truncata*) and *Mesaphorura* spp. were found at all sites.

The greatest species richness was found at Wisley Common: 38 taxa groupings whilst 23 taxa groupings were retrieved from Buxton Wood, see Table 3.4.5.1.. As for the adjacent sites a different number of soil cores were processed for the sampling occasions between April '12 and April '13, see Section 3.2.2., a valid comparison for a subset of this data is found in Table 1., Appendix 3.4.5., here the greatest species richness was still found at Wisley Common. See Figure 3.4.5.1. for species accumulation curves with all of the RHS experimental plot treatments and the sites at Wisley Common and Buxton Wood.

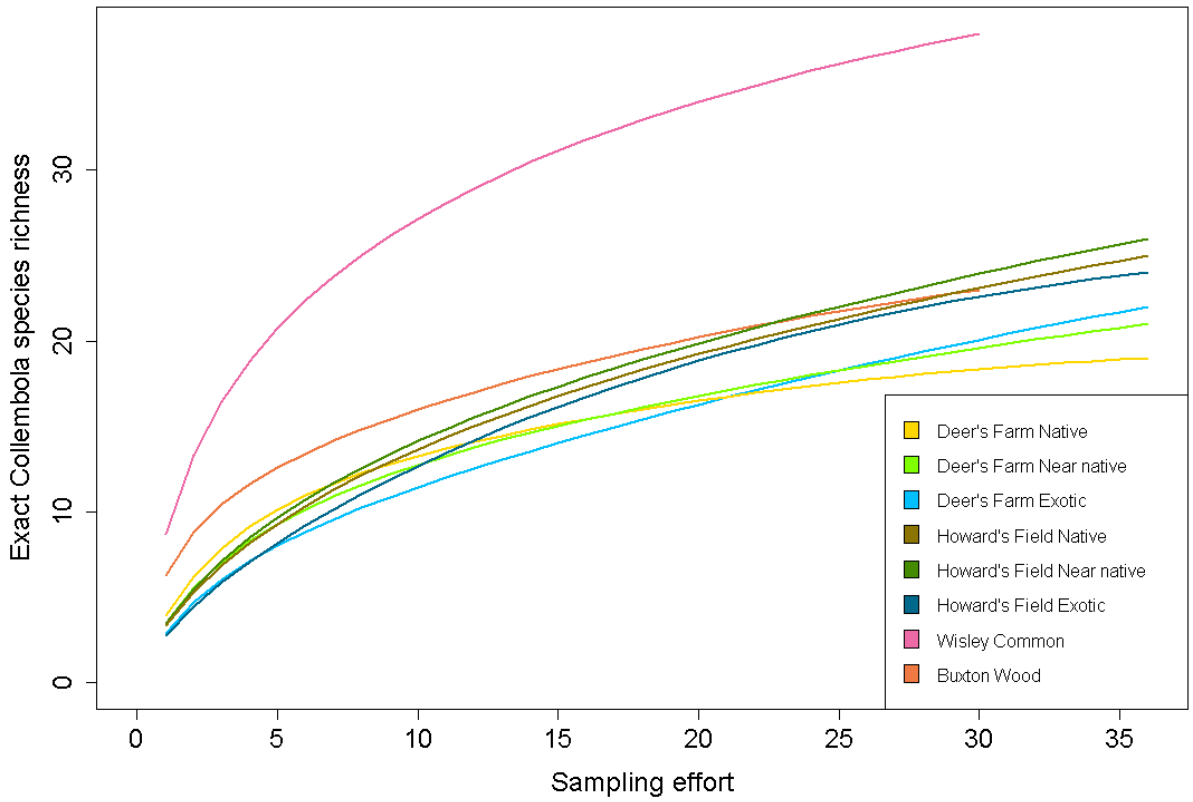

Figure 3.4.5.1. Species accumulation curves including the Wisley Common and Buxton Wood data: 30 samples (60 soil cores) each (each RHS experimental plot treatments has 36 samples (72 soil cores)).

Table 3.4.5.1. Metrics of species diversity: Species richness (R), Shannon-Weiner (H') and Gini-Simpson (1-D) for all sites: absolute species richness was calculated per site/treatment and species diversity indices per plot (pooled sampling occasion). The adjacent site metrics came from April '12 – April'13 data with one sample per occasion, other sites came from October '11 – April '13 both samples per occasion. The numbers of soil cores the figures are derived from are provided.

Site	Site/treatment	Soil cores	Total R	H'	1-D
Deer's Farm	**RHS site**	180	30	1.32 ± 0.07	0.60 ± 0.03
	Adjacent site	24	13	1.62 ± 0.06	0.72 ± 0.02
Deer's Farm	**Native**	60	19	1.32 ± 0.15	0.58 ± 0.06
	Near native	60	21	1.32 ± 0.10	0.60 ± 0.04
	Exotic	60	21	1.33 ± 0.12	0.63 ± 0.06
Howard's Field	**RHS site**	180	32	1.03 ± 0.06	0.49 ± 0.03
	Adjacent site	24	19	1.75 ± 0.09	0.72 ± 0.04
Howard's Field	**Native**	60	22	0.99 ± 0.10	0.48 ± 0.04
	Near native	60	23	0.92 ± 0.09	0.43 ± 0.05
	Exotic	60	20	1.18 ± 0.13	0.56 ± 0.05
Wisley Common		60	38	1.79 ± 0.10	0.70 ± 0.03
Buxton Wood		60	23	1.72 ± 0.04	0.76 ± 0.01

A CCA testing whether the abundances of the 37 most common Collembola differed between sites (Deer's Farm RHS experimental plots, Deer's Farm adjacent, Howard's Field RHS experimental plots, Howard's Field adjacent, Wisley Common and Buxton Wood)

found that site was a significant factor (permutation test: F = 15.882, 5 d.f., p = 0.001). See Figure 3.4.5.2. for an enlarged figure of the centre of the ordination plot and Appendix 3.4.5., Figure 1. for the full graphical representation. See Table 6. Appendix 3.4.4. for the species included.

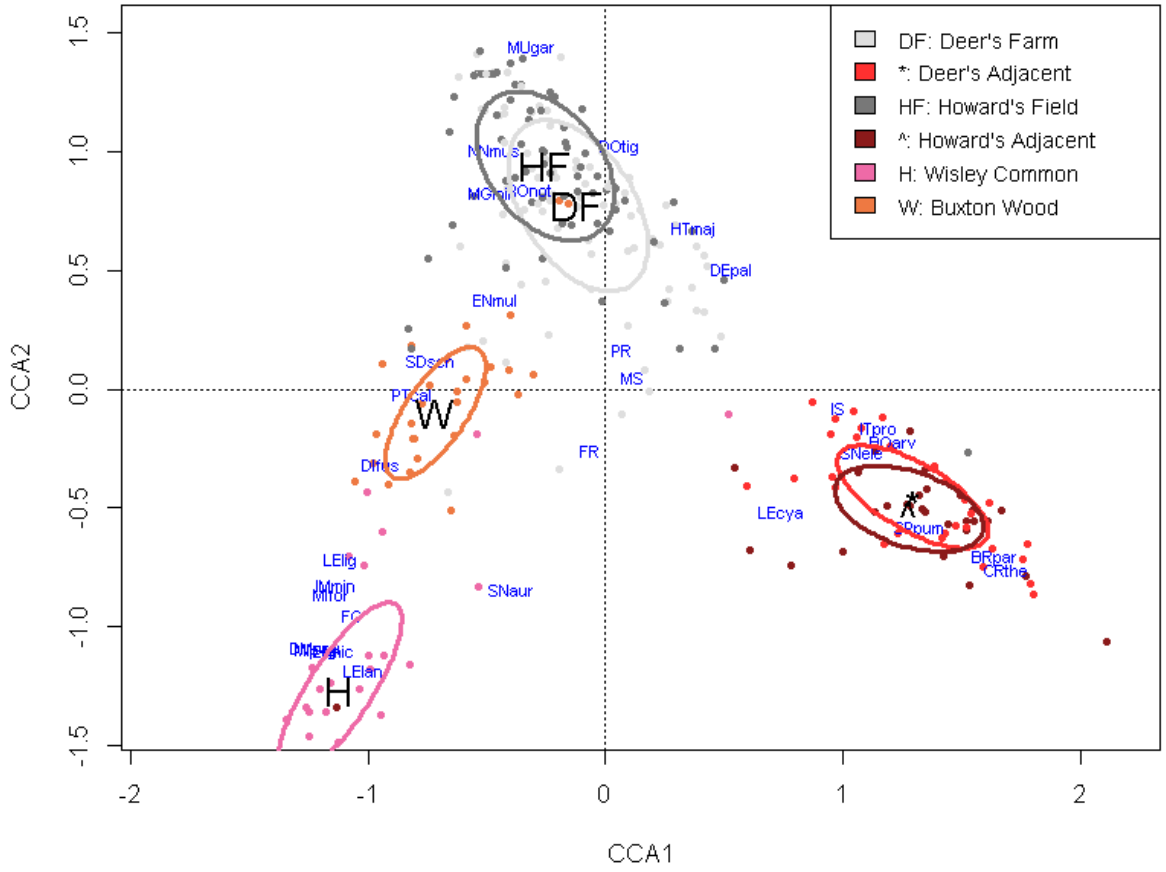

Figure 3.4.5.2. CCA ordination diagram of main Collembola species abundances (log-transformed) separated by site. Black labels represent treatment centroids: DF: Deer's Farm (RHS experimental plots), HF: Howard's Field (RHS experimental plots) *: Deer's Farm adjacent site, ^: Howard's Field adjacent site, H: Wisley Common and W: Buxton Wood. Ellipses are plotted using standard deviation from the centroids. Blue labels are Collembola species codes, see Table 2., Appendix 3.4.2., for interpretation.

Figure 3.4.5.2. cuts off several Collembola species in the bottom left hand quadrant, these fit the inclusion criteria but were predominantly (or only) found on the heath of Wisley Common: *Pseudoisotoma sensibilis*, *Tomocerus* sp., *Schoettella ununguiculata* and *Isotomurus palustris*.

In addition to season being an important factor for soil mesofauna abundance, it was also a significant factor in community composition across all sites (permutation test: F = 3.3748, 2 d.f., p = 0.001), see Figure 3.4.5.3. for a CCA ordination plot.

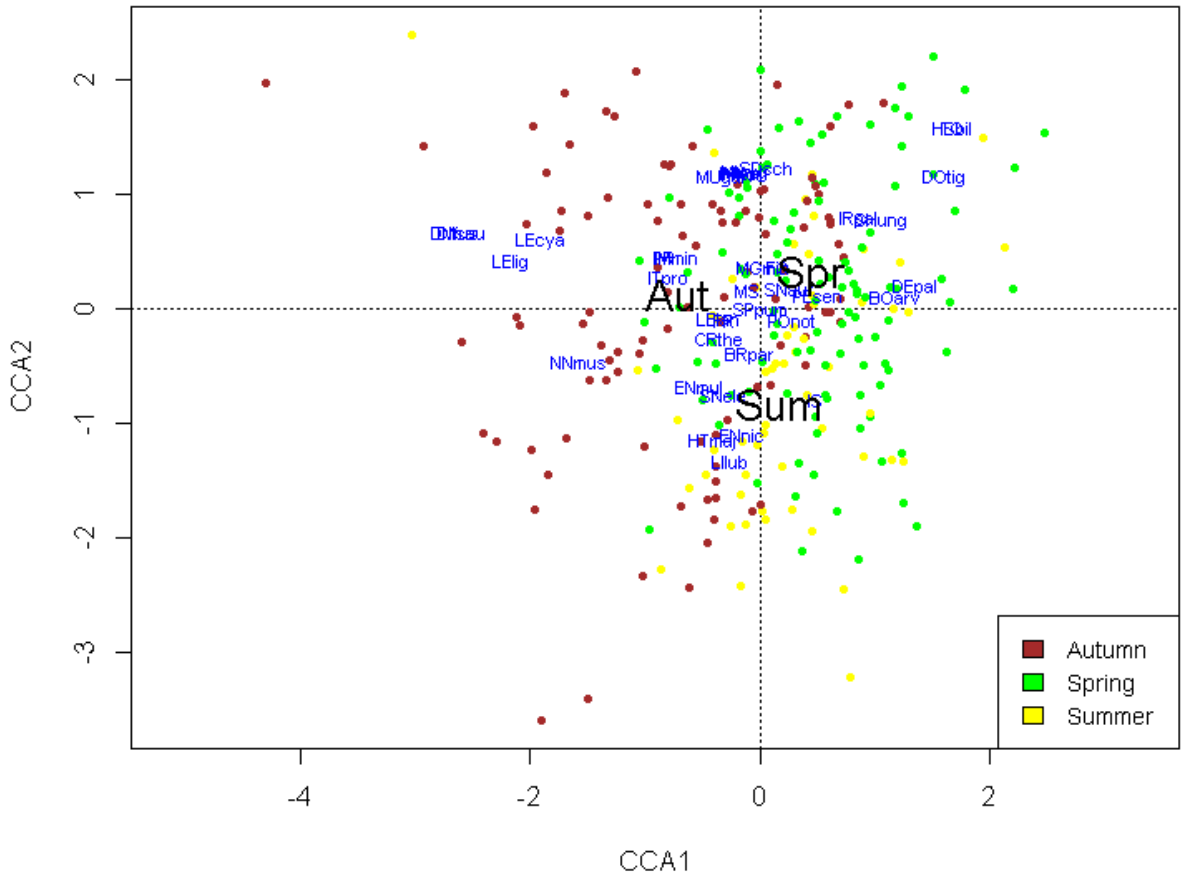

Figure 3.4.5.3. CCA ordination diagram of main Collembola species abundances (log-transformed) separated by season (Autumn: October '11 & October '12, Spring: April '12 & April '13, Summer: July '12). Black labels represent treatment centroids. Blue labels are Collembola species codes, see Table 2., Appendix 3.4.2., for interpretation.

The total species richness of a vegetation origin treatment (Native, Near native, Exotic) was greater when combined with the adjacent grassland treatment than with another vegetation origin treatment within the same site (using the data subset specified in Section 3.3.4.), see Table 3. and Table 4. Appendix 3.4.5..

A one-way ANOVA test revealed a significant difference in H' between the sites: Deer's Farm, Deer's Farm adjacent, Howard's Field, Howard's Field adjacent, Wisley Common and Buxton Wood ($F_{5, 54} = 16.16$, $p < 0.001$), see Figure 3.4.5.4. for a graphical representation. See Appendix 3.4.5., Table 6. and Appendix 3.4.5., Figure 2. for the Tukey

HSD tests and the plots of the residuals, respectively. A Dunn's post hoc test following a significant Kruskal-Wallis test revealed the same set of significant differences (Appendix 3.4.5. Tables 5. and 7.).

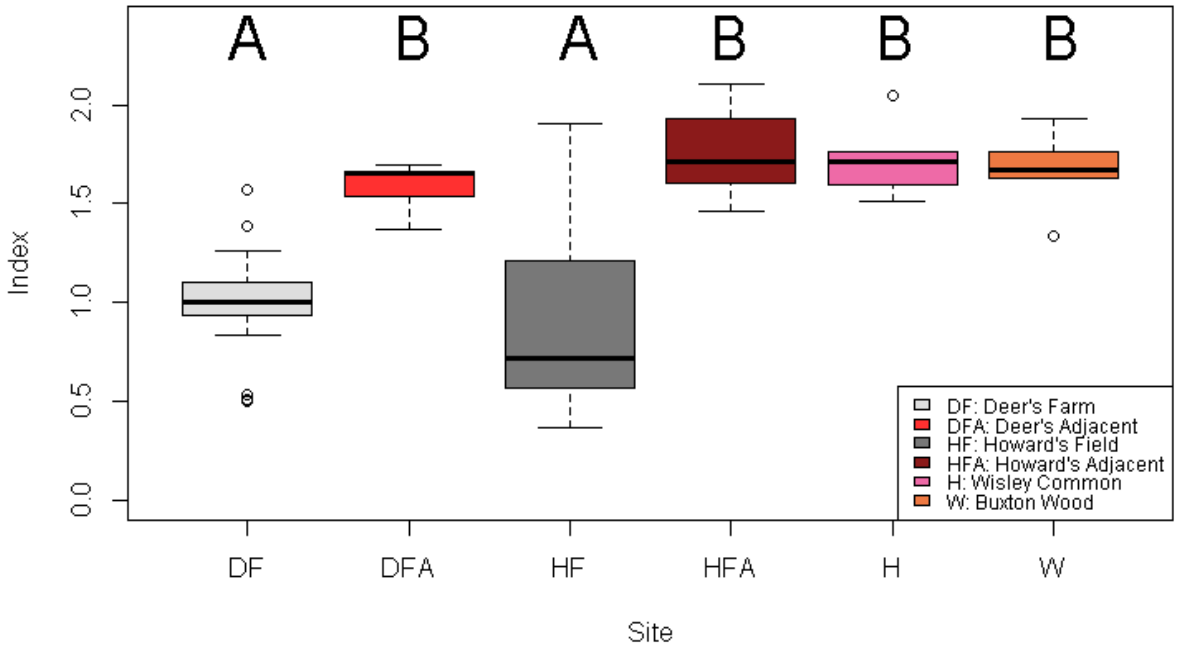

Figure 3.4.5.4. Shannon-Weiner diversity indices for all sites calculated from one randomly selected sample per sampling occasion (April '12 - April 13). Sites underneath the same letter do not differ according to the Tukey HSD post-hoc test.

A one-way ANOVA test revealed a significant difference in 1-D between the sites: Deer's Farm, Deer's Farm adjacent, Howard's Field, Howard's Field adjacent, Wisley Common and Buxton Wood ($F_{5, 54} = 11.19$, $p < 0.001$), see Figure 3.4.5.5. for a graphical representation. See Appendix 3.4.5., Table 9. and Appendix 3.4.5., Figure 3. for the Tukey HSD tests and the plots of the residuals, respectively. A Dunn's post hoc test following a significant Kruskal-Wallis test revealed a very similar set of significant differences (Appendix 3.4.5. Tables 8. and 10.).

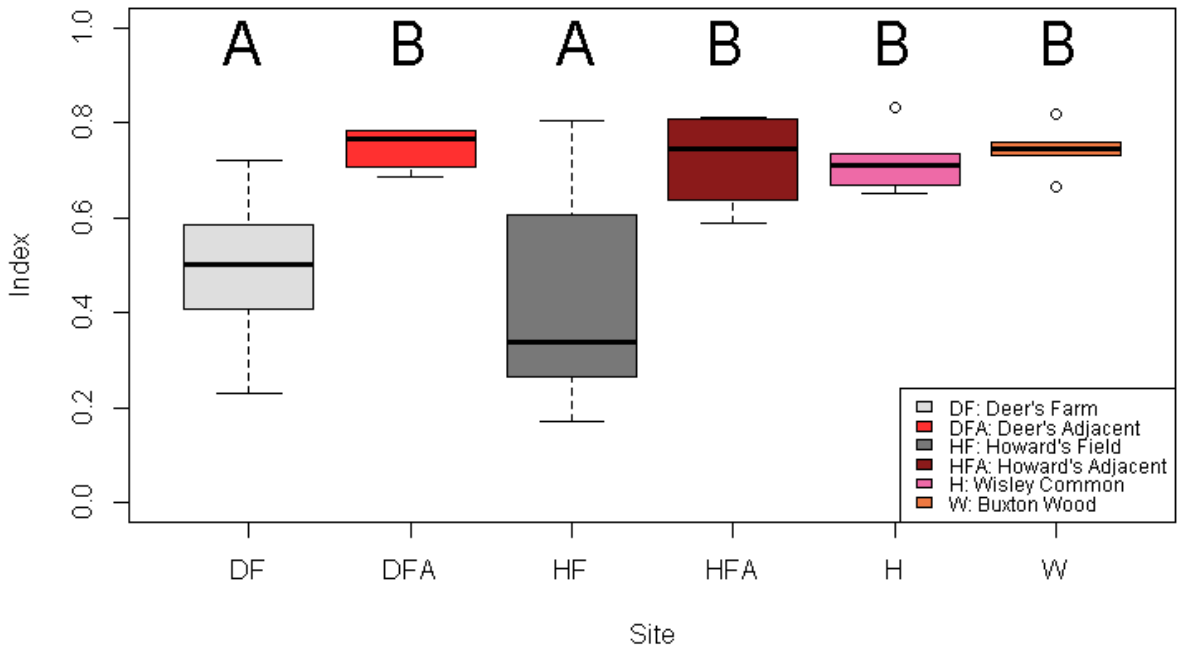

Figure 3.4.5.5. Gini-Simpson diversity indices for all sites calculated from one randomly selected sample per sampling occasion (April '12 - April 13). Sites underneath the same letter do not differ according to the Tukey HSD post-hoc test.

There were significant differences in species composition across all the sites, see Table 3.4.5.2. for the mean densities of the taxa groupings for which significant differences were found between sites (Kruskal-Wallis test $p < 0.05$ (see Table 2., Appendix 3.4.5. for results from all taxa)).

Table 3.4.5.2. Summary data for Collembola mean density (kg-1) per site ± standard error, with significance of between site effects calculated by the Kruskal-Wallis test (only significant results presented). See Table 2. Appendix 3.4.2. for interpretation of species codes and Table 2. Appendix 3.4.5. for full results.

	Deer's Farm	Howards Field	Deer's Adjacent	Howard's Adjacent	Wisley Common	Buxton Wood	Site effect
CRthe	0.03 ± 0.03	-	29.3 ± 9.26	89.45 ± 24.82	-	-	***
FOspp.	0.67 ± 0.64	0.69 ± 0.4	-	0.94 ± 0.6	73.76 ± 12.72	39.93 ± 7.8	***
ISspp.	1.41 ± 0.46	1.01 ± 0.43	26.61 ± 6.88	20.59 ± 4.93	0.53 ± 0.45	0.09 ± 0.09	***
IMmin	-	0.07 ± 0.04	-	-	2.91 ± 1.25	3.63 ± 0.85	***
ITpro	0.77 ± 0.42	0.1 ± 0.06	15.28 ± 13.08	17.33 ± 8.51	-	-	**
Irpal	-	-	-	-	2.84 ± 1.22	-	***
POnot	31.52 ± 5.03	35.57 ± 5.46	7.4 ± 3.01	3.21 ± 1.35	7.57 ± 2.7	39.72 ± 2.99	***
PEsen	-	-	-	-	21.99 ± 3.83	0.09 ± 0.09	***
TOsp.	-	-	-	-	0.44 ± 0.22	-	***
CYalb	-	-	-	0.72 ± 0.43	-	-	***
ENmul	0.83 ± 0.21	0.43 ± 0.13	0.25 ± 0.17	-	1.59 ± 0.17	-	***
ENnic	0.08 ± 0.04	0.07 ± 0.07	-	-	1.43 ± 0.33	-	***
HTmaj	1.12 ± 0.31	0.59 ± 0.26	1.72 ± 0.57	1.7 ± 0.54	-	-	**
LEcya	0.12 ± 0.07	0.03 ± 0.03	3.18 ± 0.88	0.1 ± 0.1	0.71 ± 0.48	-	***

LElan	0.25 ± 0.11	0.02 ± 0.02	0.81 ± 0.33	-	11.6 ± 1.89	2.53 ± 0.6	***
LElig	-	-	-	-	0.37 ± 0.19	2.2 ± 0.84	***
SHung	-	-	-	-	1.6 ± 1.12	-	**
BRpar	0.05 ± 0.04	-	3.38 ± 0.72	6.74 ± 1.51	-	-	***
FRspp.	0.77 ± 0.25	0.27 ± 0.2	1.07 ± 0.96	6.46 ± 1.59	3.62 ± 2.06	15.07 ± 9.1	***
MIfor	-	-	-	-	0.5 ± 0.29	0.79 ± 0.27	***
MIpyg	-	-	-	-	0.99 ± 0.42	1.6 ± 1.05	***
PRspp.	0.6 ± 0.2	0.09 ± 0.04	-	3.38 ± 1.36	-	3.36 ± 1.77	**
MSspp.	3.26 ± 0.54	1.42 ± 0.31	6.46 ± 1.5	10.62 ± 1.52	4.95 ± 0.77	7.81 ± 0.72	***
SNaur	0.05 ± 0.05	0.05 ± 0.05	0.11 ± 0.11	0.9 ± 0.9	0.92 ± 0.23	0.64 ± 0.42	**
SNele	0.2 ± 0.09	0.34 ± 0.19	0.92 ± 0.38	5.06 ± 1.06	0.23 ± 0.16	-	***
LIlub	-	-	-	-	0.66 ± 0.46	-	**
SMnig	-	-	-	-	0.13 ± 0.08	-	**
SPpum	0.26 ± 0.1	0.18 ± 0.07	16.62 ± 4	19.07 ± 4.42	1.26 ± 0.86	-	***
BOarv	-	0.16 ± 0.12	1 ± 0.33	0.69 ± 0.31	-	-	***
DEpal	0.57 ± 0.21	0.57 ± 0.24	1.09 ± 0.6	3.2 ± 2.17	-	-	*
HSbil	-	-	-	-	0.6 ± 0.21	-	***
DIfus	-	0.1 ± 0.06	-	-	0.39 ± 0.18	0.18 ± 0.11	*
DMsau	-	-	-	-	0.16 ± 0.11	0.23 ± 0.15	**
MGmin	9.56 ± 2.4	11.72 ± 3.43	-	-	4.66 ± 2.03	14.73 ± 1.75	***

-: Not recorded, NS: $p > 0.05$, *: $p < 0.05$, **: $p < 0.01$

In this dataset July '11 was excluded; *P. notabilis* was still found to be the Collembola present at the greatest densities in both the Deer's Farm and Howard's Field RHS experimental plots. This species was present at all of the sites, but at significantly different densities (Kruskal-Wallis: $\chi^2 = 31.06$, 5 d.f., $p < 0.001$). *F. quadrioculata* 'group' was the Collembola grouping found at the greatest densities at both Wisley Common and Buxton Wood, it was present at three of the other four sites, but at significantly lower densities (Kruskal-Wallis: $\chi^2 = 41.72$, 5 d.f., $p < 0.001$).

The Collembola *Megalothorax minimus* and *Cryptopygus thermophilus* showed a marked difference in distribution between the RHS experimental sites and their adjacent grassland, this was significant across all sites for both *M. minimus* (Kruskal-Wallis: $\chi^2 = 30.69$, 5 d.f., $p < 0.001$) and *C. thermophilus* (Kruskal-Wallis: $\chi^2 = 55.02$, 5 d.f., $p < 0.001$). See Figure 3.4.5.6. for a graphical representation of these species at Deer's Farm and for

Howard's Field see Figure 3.4.5.7.. *M. minimus* was the second most abundant species from the RHS experimental plots but was absent from the adjacent grassland, whereas *C. thermophilus* was the species present in the greatest densities at both the adjacent sites yet very few individuals were retrieved from any of the RHS experimental plots.

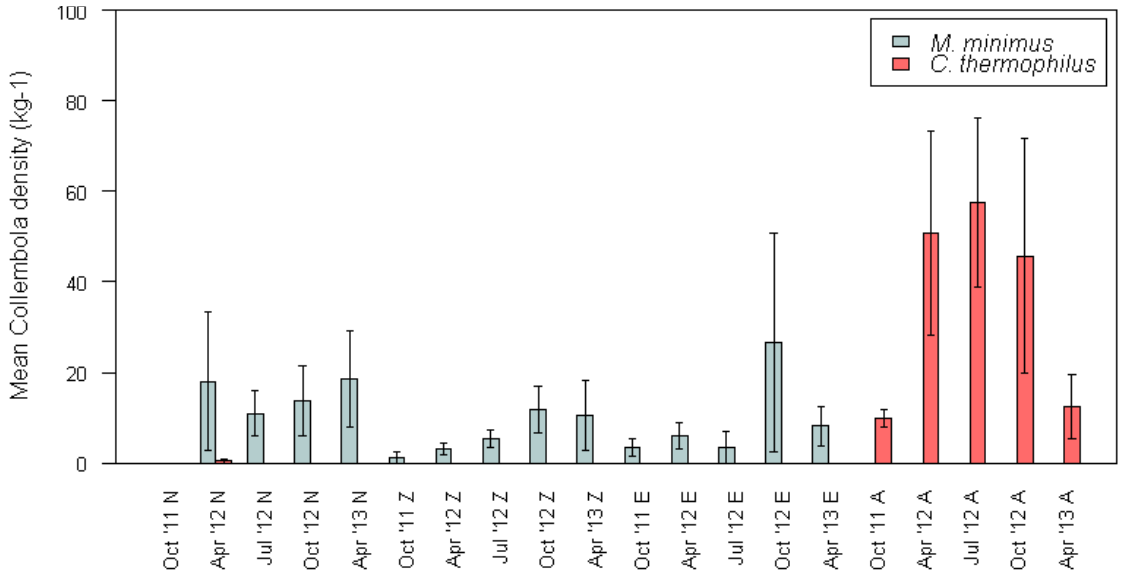

Figure 3.4.5.6. Barchart of the mean density of *Megalothorax minimus* and *Cryptopygus thermophilus* (kg-1) at Deer's Farm, for all RHS experimental plot treatments (Native: N, Near native: Z, Exotic: E) and the adjacent grassland: A, for the 5 sampling occasions between October '11 and April '13. *M. minimus* and *C. thermophilus* density represented by blue and red bars, respectively. Error bars plotted using the standard error.

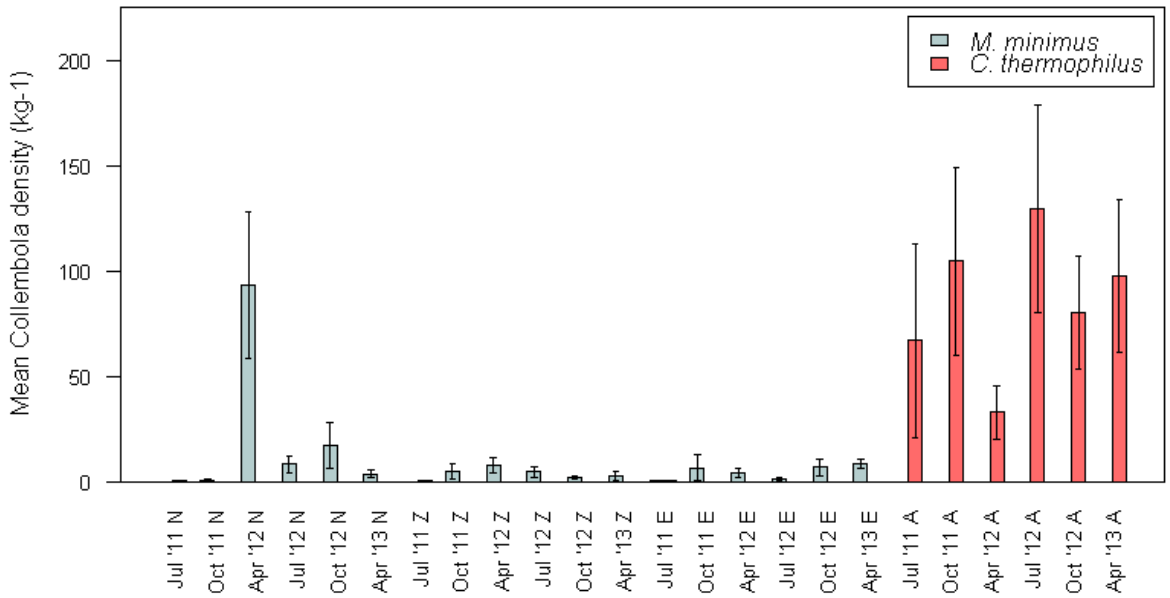

Figure 3.4.5.7. Barchart of the mean density of *Megalothorax minimus* and *Cryptopygus thermophilus* (kg-1) at Howard's Field, for all RHS experimental plot treatments (Native: N, Near native: Z, Exotic: E) and the adjacent grassland: A, for the 5 sampling occasions between July '11 and April '13. *M. minimus* and *C. thermophilus* density represented by blue and red bars, respectively. Error bars plotted using the standard error.

3.5. Discussion

3.5.1. Soil fauna abundance

3.5.1.1. Collembola abundance

In this study the vegetation origin treatment, season, soil moisture and the interaction between soil moisture and season were found to be important factors in explaining differences in Collembola abundance.

The significant effect of treatment is not likely to be due to differences in soil properties of the plots planted with the different vegetation origin treatments. Aside from the one explainable exception of Mg, no significant differences in the other soil properties (P, K and soil organic content) were found between the plots, see Chapter 2., Sections 2.4 and 2.5.2..

It could be that the effects of treatment are explained by differences in vegetation properties. Vegetation density and canopy cover of the RHS experimental plots varied, across all treatments, according to season as some of the plants used were deciduous; e.g. *Rosa rubiginosa*, whilst others are spring-flowering herbaceous perennials; e.g. *Hyacinthoides* spp.. There could have been a difference in vernalisation and overall vegetation cover between the different origin treatments, see Chapter 1., Section 1.9. for literature regarding the effects of vegetation cover on soil fauna, and this could have varied with season. If there were differences in the vegetation structure between the different vegetation origin treatments this could explain the significant treatment effect on abundance. Though the vegetation percentage cover recording dates do not match exactly with the soil core sampling periods it can be seen that there was variation in percentage cover, within season, across both the RHS experimental plot sites, see Table

3., Appendix 3.2.. With the soil core sampling location being randomly selected from within the plots, for those that had a larger percentage of bare ground, the soil core would have been more likely to have been retrieved from exposed co-ordinates. Collembola populations were adversely affected in a study where all plants were removed from a perennial grassland, which would have left bare ground, and were unaffected in treatments where only one functional group of plants was removed (Wardle et al. 1999). Vegetation cover, especially where it is dense, will reflect a percentage of the solar radiation. Increases in vegetation density/cover are likely to temper temperature fluctuation of the air and soil beneath them; also lowering wind speeds and air movement making the air moister through the reduced removal of water lost through transpiration and evaporation at the soil surface. The soil temperature of the bare ground is likely to reach higher levels and fluctuate more during the day as shadows created by the vegetation move across the bare ground due to the changing position of the sun. This will relate to a difference in microclimate. Soil moisture was recorded as a co-variate and it was found to be a significant factor in explaining the variation In Collembola abundance, but a difference in microclimate would encompass other parameters: e.g. soil temperature (which has been found to affect soil fauna feeding activity (Gongalsky et al., 2008), light climate, and the variability of these conditions over the course of a day (vegetation cover/density would provide a buffering effect, possibly limiting extremes and evaporation (Moran et al., 1996)).

In this experiment the greatest numerical abundances were found, on average, in the spring. In other work, peak abundances for Collembola are observed in the autumn; Fountain and Hopkins (2003) found that abundances of Collembola were too low in the spring and summer months for analysis with species distributions fitted only to the

autumn data, however, Usher, Booth, and Sparkes (1982) were able to perform multivariate analysis on data collected for all seasons apart from winter. This seasonality is exhibited by the euedaphic species in particular, however, this could be due to the associated environmental conditions generally experienced during those seasons; a result of the rainfall and subsequent soil moisture levels. October ’11 was dryer than July ’11 with 25 mm and 45.8 mm of rain being recorded from the Deer’s Farm weather station, respectively (see Table 2., Appendix 3.2.). For October ’11 this was only 33 - 50% of the average amount of rainfall for this period in Surrey; it was unusually dry (Met Office 2011). In a review (Petersen & Luxton, 1982) on Collembola density from a range of habitats and biomes, Collembola densities were found to be lowest in soils classified as dry; they are known to be susceptible to desiccation at low moisture levels (see Chapter 1., Section 1.7.3.). The dry October was then followed by a very wet April ’12, the Deer’s Farm weather station recorded almost four times as much rainfall for this month: 96.6mm of rain, this was over 200% of the average amount of rainfall normally expected for this period (Met Office 2012). July ’12 was also wetter than October ‘11 (Deer’s Farm weather data = 64.8 mm rain).

For nine plots no Collembola were retrieved for a sampling occasion. A total of 216 soil cores were collected from the RHS experimental plots, so whilst this is slightly unusual this soil faunal group were only absent from 4% of the samples collected. Five of these Collembola absences occurred in the July ’11 sampling occasion (summer), when Collembola abundances are expected to be lower, with two more absences in October ’11 which was an unusually dry period, see above. Of the remaining two occasions Collembola were absent from one plot in July ’12 (also a summer sampling occasion) and

another in October ’12. Only one plot recorded no Collembola for two occasions (plot H5EB).

The Collembola models were run without the data retrieved from plot H2ZB, October ’12. This point was found to be approaching Cook’s distance when it was included in exploratory models. It represented an unusually high number of Collembola, 220 individuals, 26% of the total Collembola retrieved from all planting treatments at both RHS experimental sites for that sampling occasion. 202 of these were the same Collembola species: *Willemia intermedia*, this was, in itself, unusual. This species was only retrieved from one other soil core (the same plot, July ’12).

Willemia intermedia is considered a rare species with there being few records (Hopkin & Shaw, 2014). There was only one confirmed record from Berkshire in 1972 which was determined by Hopkin (Hopkin, 2007). It is possible that this species is under recorded as it is very small with specimens needing to be cleared carefully for the PAO arrangement to be observed clearly and for the time-pressed or non-diligent collembologist it is not hard to imagine it being mistaken for the apparently common and widespread *Willemia anopthalma* (also recorded in this study).

The Collembola densities were significantly greater for the adjacent grassland than for the RHS experimental plots at both Deer’s Farm and Howard’s Field. These plots are situated very close together, in fact some of the RHS experimental plots are closer to the adjacent plots than they are to other plots under the same vegetation origin treatment (at the same site). The differences between the RHS experimental plots and their adjacent grassland could be a result of management, they have been treated as flowerbeds;

fertilised and disturbed via weeding/planting accordingly. The vegetation cover observations for the RHS experimental plots (Table 3., Appendix 3.2.) even though they do not match up exactly with the soil core sampling periods document that bare ground was recorded for some of the plots, this contrasts with the adjacent grassland where the ground was completely covered by low growing plants (see Chapter 2., Section 2.1.3.). This difference in vegetation structure between the RHS experimental plots and their adjacent grassland is likely to have resulted in a different microclimate at the soil surface and the upper layers of the soil profile. See the discussion of vegetation cover/bare ground in relation to explaining the differences observed in Collembola abundance between the vegetation origin treatments earlier in this section. The fact that Collembola densities can be high in the soil of grassland habitats has been noted (Stanton, 1988), but in the soil biodiversity assessment component of the Countryside Survey 2000, Collembola were more frequently recorded in soil cores collected from woodland habitats and least frequently in those retrieved from infertile grassland, moorland and heathland (Black et al. 2003), which agrees with the work of Petersen and Luxton (1982) who found a higher proportion of low Collembola densities in temperate grasslands than temperate forests, and Fierer et al. (2009) who observed the same pattern with regards to Collembola biomass. The majority of the published literature, on the comparison of UK grassland Collembola densities, has looked at the conversion from agricultural land use to grassland (Chauvat et al. 2003), varying degrees of land use intensity in agricultural settings (e.g. Bardgett & Cook (1998); Sousa et al. (2006)) (including studies looking at the applications of fertilisers) or the effects of plant species richness (e.g. Sabais, Scheu, & Eisenhauer (2011); Salamon et al. (2004)). There has been little work on the comparison between flowerbed type habitats and grasslands and none within a garden context. The RHS experimental plots were probably more similar to the heathland in terms of

vegetation structure, but with greater management and a higher percentage of bare ground; low input agricultural crop land could represent the most equivalent habitat within the literature, in which case an increase in Collembola abundance/density from this habitat to grassland could be expected (see Chauvat et al. (2003)).

It should also be recalled that the RHS experimental plots are 3 m x 3 m, this was because they were intended to represent a typical garden border in size and area (see Salisbury et al., 2015; Smith et al., 2006). Although each adjacent plot was placed under the same dimensional constraints, the demarcation between 'plot' and 'non plot' differed. The RHS experimental plots were surrounded by wooden borders, which were drilled with 25 mm holes at 25 mm intervals to allow movement of ground fauna, separated by a 1 metre wide woodchip covered guard row (Salisbury et al., 2015). This meant that each plot was separated and surrounded by a different microhabitat which could have hindered Collembola dispersion between plots, and they were also subject to any edge effects on all sides. In comparison the adjacent plots were not subject to such marked edges. The adjacent plots were taken from a continuous, unfragmented, piece of grassland with no barriers to movement, this is also true of the heath and wood plots.

Wisley Common and Buxton Wood were not included in the abundance models, however, from Figure 3.4.2.5. it can be seen that the Collembola densities for these sites were greater than those found in the RHS experimental plots, with the possible exception of July '12. In a review of global soil fauna populations, Petersen and Luxton (1982) found no overall difference in Collembola density between wooded and non-wooded sites, though they, and other authors, found evidence suggesting that greater densities could be expected from woodlands (Black et al. 2003; Petersen & Luxton 1982; Fierer et al. 2009).

Here, although the data were not analysed, the Collembola densities found at the grassland, heathland and woodland sites appear to be similar; the error bars overlap and there are no consistent differences (Figure 3.4.2.5.). The habitat quality of Buxton Wood is discussed in relation to the results obtained from the Collembola species diversity analysis (Section 3.5.2.2.), and it could be that the same arguments made there apply here; lower densities may have been found due to the hang-over influence of previous land-use. This is only the abundance of one component of the soil fauna to get a better picture more than one taxa needs to be considered.

3.5.1.2. Acari abundance

In the Acari abundance models pH, season, vegetation origin treatment, and the interaction between season and vegetation origin treatment were found to be important factors for explaining the variation in abundances.

As discussed in Section 3.5.1.1., vegetation cover was observed to vary with season and there could be a difference in that provided by the vegetation origin treatments which may also have varied with season resulting in differences in microclimates between treatments. Vegetation cover has previously been shown to affect Acari populations: both abundance and diversity were found to be higher in unmown than mown treatments (Mailloux et al., 2010).

The soil macronutrients measured in Chapter 2. do not explain the significant effect of vegetation treatment on Acari abundance, the discussion for this is the same as that made regarding the Collembola, see Section 3.5.1.1., however pH was found to be the most important factor included in the models in determining Acari abundance. It has

previously been found to be a significant factor in predicting Acari densities, with pHs between 5 and 6 being associated with average Acari densities and sites with a pH lower than 5 having, on average, higher density Acari populations (see Petersen & Luxton (1982)). Mulder et al. (2005) also found pH explained much of the variation in numerical abundance of Acari between different sites. For the RHS experimental sites, Howard's Field was significantly more acidic than Deer's Farm (see Chapter 2., Section 2.4.1.), with mean pH values of 6.2 and 7.7, respectively, and it was at Howard's that the higher Acari abundances were recorded.

There were significant differences in Acari density (kg-1) across both the RHS experimental sites and their adjacent grasslands. Given that pH was an important factor in the RHS experimental plot Acari abundance models, it could explain some of the differences in Acari density observed here. The Acari densities of the Deer's Farm RHS experimental plots were significantly lower than all of the other sites and this site did also have the highest pH values (see Chapter 2., Section 2.4.1.), though this does not account for the significant difference in Acari density observed between the Howard's Field RHS experimental site and its adjacent grassland (as there was no difference in pH here), but this could have been due to additional differences in vegetation cover between the RHS experimental plots and the grasslands; as mentioned regarding the discussion of the significant effect of vegetation origin treatment Mailloux et al. (2010) found that vegetation cover influenced Acari abundance. There were also other parameters that were not recorded or measured, that could have had an effect, e.g. soil compaction or availability of other soil macronutrients (aside from N, Mg, P, K or LOI).

When all sites were considered, Acari density patterns were similar to those of the Collembola, with greater densities generally observed at the grassland, heathland and woodland sites than for the RHS experimental plots. Aside from the relatively high densities obtained from the grasslands this is consistent with the findings of Black et al. (2003) who recorded Acari most frequently from woodland and heathland soil cores (as well as moorland).

Both Acari and Collembola were found under all vegetation origin treatments and at all sites, though their densities differed, this could be related to disturbance and/or differences in management. However, this is just one aspect of biodiversity and does not answer whether the plots or sites differed in terms of diversity, so lower taxonomic levels need to be explored.

3.5.2. Soil fauna diversity

3.5.2.1. Collembola diversity: RHS experimental plots

Two diversity indices were calculated: Shannon-Weiner (H') and the Gini-Simpson index (1-D), these measure species evenness and dominance concentration, respectively. Greater H' values indicate a more even distribution in the abundance of the species present and as 1-D gives the probability that two randomly selected Collembola will be of different species which means that higher values indicate a more diverse community. There was a greater difference in Collembola species diversity, from both these indices, between the two RHS experimental sites than between the vegetation origin treatments. There was no statistically significant difference in the diversity indices calculated between the vegetation origin treatments, see Table 3.4.4.1., Section 3.4.4. of this chapter.

For the RHS experimental plots the Collembola species richness was greater at Howard's Field than Deer's Farm, but within each site there was no statistically significant difference in total species number between the different vegetation origin treatments. The species diversity of the RHS experimental plots was lower than that of the adjacent grassland and the semi-natural habitats (when a subset of the data was analysed to ensure equivalency), this is discussed in Section 3.5.2.2.. It is worth mentioning that the observed Collembola diversity is still undeniably greater than that found for green roofs, which are very drought stressed systems; 5 species (Rumble & Gange 2013) and both are presumably greater than the alternative of no lawn and no green roof, this is discussed further in Chapter 6., Section 6.1.1..

The CCA exploring the effect of vegetation origin treatment on the main species (Figure 3.4.4.4.) of Collembola present across the RHS experimental plots did find a difference in community composition; however, it did not include all of the species found (20 out of 44). It suggests that there are differences in the abundances of Collembola species between the treatments, though when ellipses were plotted using the standard deviation there was a large amount of overlap and combined with the results of the Kruskal-Wallis tests (Table 3.4.4.2.), any difference between the Collembola communities is not strong and preferences are not apparent for all species. Differences indicated here could in part be a result of the number of Collembola unidentifiable to the required level as these were excluded from the analysis e.g. *Entomobrya* sp., see Section 3.3.4.. The CCA which covered the Collembola diversity data across all sites (see Section 3.4.5. and Figure 3.4.5.2.) had more species meeting inclusion criteria and will be discussed further on.

For the diversity analysis it was also necessary to group several species at the genus level: *Friesea* spp. *Mesaphorura* spp., *Protaphorura* spp., *Isotoma* spp. and *Folsomia quadrioculata* 'group' (see Section 3.2.2.). Within the literature on Collembola taxa groupings have previously been used e.g. *Mesaphorura* spp. by Shaw (2003) and *Sminthurides* spp. by Shaw (1997). In this study grouping could have affected the species richness totals, though for the *Protaphorura* and *Mesaphorura* many individuals were still identified with only one species being found in each case (*P. armata* and *M. marcrocheata*). For two of the other taxa groupings (*Friesea* spp. and *Isotoma* spp.); *F. claviseta*, *F. mirabilis*, *F. truncata*, *I. anglicana* and *I. viridis* were found under all treatments so the grouping would not have made a difference to the relative species richness. For the final grouped taxa: *F. quadrioculata* 'group' positive identification to species level was not easy and if separation into *F. manolachei* and *F. quadrioculata* had been attempted for all individuals there would still have been a large proportion where identification was uncertain that would have remained grouped at the genus level.

When Kruskal-Wallis tests were performed on the densities of separate Collembola species found under the different vegetation origin treatments of the RHS experimental plots: significant differences were found for *Hetermurus major* and *Sphaeridia pumilis* in the autumn and *H. major* and *P. notabilis* in the summer, this was out of the total 44 species analysed and for each of the seasons separately. There were no differences in species distribution across the treatments in spring. Overall this meant that less than 7% of the Collembola species showed a preference between the vegetation origin treatments and that where there was a difference that this was not consistent across all seasons. It suggests that Collembola community composition was similar under all the vegetation origin planting treatments.

Until recently it was not established that *H. major* was present in the UK; it does not feature in the AIDGAP Collembola key (Hopkin 2007), but since then it has been recorded in the above ground sampling effort of the 'Plants for Bugs' project (Hopkin & P. Shaw 2013a). It would be interesting to see if the distribution pattern of this species is also observed for the vortis and pitfall sampling of the 'Plants for Bugs' project, as *H. major* is generally considered to be an epiedaphic species, if there really are vegetation origin differences for this species they should be more apparent using these sampling strategies. The same is true for *S. pumilis* which is also a surface active species; it has been associated with grasslands (Chauvat et al. 2007), so it could be useful for the data for this species to be considered along with vegetation cover and density parameters.

Within the RHS experimental plots the dominant species was found to be *P. notabilis* (formerly *Isotoma notabilis*), which was found under all treatments, at all sites and all sampling occasions. It is known to be tolerant of a wide range of conditions from its presence as one of only six species found to be able to colonise green roofs in urban areas (Rumble & Gange 2013), one of only four species to be found at a range of polluted urban sites (Fountain & Hopkin, 2004) and in other studies has accounted for over half the number of Collembola retrieved (Poole 1962). It has previously been classified as alkalophilous (see van Straalen & Verhoef (1997)) here in addition to being present at the Deer's Farm experimental plots (mean pH: 7.7) it was also found at the strongly acidic sites of Wisley Common and Buxton Wood, mean pH 4.2 and pH 4, respectively (NRM analysis, see Chapter 2., Section 2.4.1.). It is a notoriously ubiquitous and it is worth recalling here that it has recently been established that *P. notabilis* is likely to be a polyphyletic taxon (Porco et al., 2012) (see Chapter 1., Section 1.5.4. and Chapter 4.,

Section 4.1.3.). It could be that several of the proposed lineages have been found here, the likelihood of this is discussed further in Chapter 4..

In addition to the diversity indices calculated here another way of exploring communities is through the analysis of functional diversity e.g. following Faber, (1991) who separated the Collembola into feeding guilds based on fungal feeding habits. Where for some Collembola this would not have been possible to determine from the literature a carbohydrase analysis of the gut contents could have been used to establish what individuals had been feeding on (e.g. Mulder et al., 2011). Due to time constraints this was not considered for this study.

Aside from the *W. intermedia* (see Section 3.5.1.1.) there were a couple of Symphypleona retrieved from the RHS experimental plot soil cores that are worth mentioning, although they were found at very low levels. *Katiannia schoetti* is a Collembola species native to the southern hemisphere and has previously been recorded from other horticultural settings; the Lost Gardens of Heligan (Cornwall), Sheffield Botanic Gardens (South Yorkshire) as well as the RHS experimental plots at Wisley and it has been speculated that this is the result of accidental importation (Ardron, 2009; Hopkin & Shaw, 2014). The same could be true of the other exotic *Katiannia* sp. ('*Katianna* species 4') found in the RHS experimental plots; three specimens were collected from Heligan in 2009 (Ardron 2009). There have been other suspected cases of Collembola entering the UK through association with horticultural materials (Shaw, 2009) and it has been documented, as a means of introduction, for other invertebrates.

Live plant imports have been identified as a major introduction pathway for species that went on to become invasive; it accounted for approximately 70% of the damaging insect species and pathogens of forest in the US between 1860 and 2006 (Liebhold etal., 2012). In the UK, by 2000, 340 of 8893 species of insects and mites on the British phytophagous insects database were non-native (Manchester & Bullock, 2000 cite Ward pers. comm.) and this number is likely to have increased. For UK non-native plant pests between 1970 and 2004 of 164 establishments 114 were found to be human assisted, with 90% a result of plant trade (Smith et al., 2007).

The extent of the spread of these exotic Collembola species is unknown, they may currently be confined to places they have directly been transferred too, such as these well-known horticultural gardens or it could also be that it is in these situations that species are more likely to be encountered or looked for and exotics noted and recorded. This is despite the phytosanitary requirements that need to be met for a plant to be imported from outside the EU and some requirements within the EU. None of the plants used in the vegetation origin treatments came directly from abroad, so there could already be existing populations at the garden centres and nurseries that supplied the project. This has several implications: non-native arthropods are currently living in nurseries which could possibly facilitate garden range expansion and lead to naturalisation; even if the non-native plant species themselves do not escape the confines of the garden their accompanying soil fauna is much less visible and harder to determine the fate of. According to invasion statistics only one tenth of the species that are introduced become established/naturalised and it is only the same fraction again of these that are likely to become a pest species (Williamson & Fitter 1996), what is known is that

if something is never introduced then it will not have the opportunity to become established and the possibility of going on to become a pest.

It could be informative to monitor or document any range expansion of these Collembola species. At the moment they have only been retrieved from the soil cores collected from the RHS experimental plots at Howard's Field; from the plots with the near native and exotic vegetation. The vegetation for the plots was planted between May 2009 and June 2010 with exotic Collembola being recorded from the October '12 sampling occasion and the last sampling occasion in April '13. This means that if they arrived at the site via the vegetation that they have been present and survived there a minimum of 2 years 9 months, possibly enough time for multiple generations or maybe even to become an established population? Most Symphypleona exhibit an epiedaphic lifestyle being primarily surface dwelling and are seldom found within the soil (Hopkin, 1997), which means that for a fuller representation of the abundance of these species here alternative sampling methods should be used; the pitfall and vortis sampling conducted as part of the 'Plants for Bugs' project should reveal a more accurate picture of their presence.

3.5.2.2. Collembola diversity: All sites

The species diversity indices (H' 1-D) were not significantly different between the Deer's Farm adjacent grassland, the Howard's Field adjacent grassland, Wisley Common and Buxton Wood, but all were significantly greater than those calculated for the RHS experimental plots. The CCA conducted on the 37 most common Collembola species/taxa groupings across all sites found that different communities were present at the different sites. The two RHS experimental sites appear to be more similar to each other in terms of species composition than they were to the adjacent grassland immediately beside them,

see Figure 3.4.5.2. The CCA plot does show a degree of arching, this 'horseshoe effect' is frequently encountered in the ordination plots of ecological data and should not be considered an artefact where there is a high species turnover (change in species composition between one community and the next) between sites (Podani & Miklós 2002), it is interesting because it shows that the Collembola soil communities are very different between all the habitats. The majority of the Collembola species found exhibited significant differences in density across all sites, see Table 3.4.5.2., this difference in community composition is not unexpected, the differences between heathland and pastureland are well established (e.g. Ponge et al. (2008)).

When the sites of Wisley Common and Buxton Wood were considered this was to provide a window into possible communities that could be supported if the RHS experimental sites had not been converted to a garden. Sites were as close together as possible, whilst still belonging to a different habitat, so the soil properties were as similar as possible, however, there were significant differences in the macronutrients measured, see Chapter 2.. The most notable difference between the RHS experimental plots and the other sites was in Mg and K where the RHS experimental plots tended to have significantly greater availability of these macronutrients, especially when compared to Wisley Common and Buxton Wood. The soil of Buxton Wood had significantly higher levels of $NO3^-$ whilst Wisley Common had comparatively low P availability (see Chapter 2., Section 2.4.). It could be that the increased levels of macronutrients have driven Collembola diversity down, *P. notabilis* is a ubiquitous species and the soil environment created in the RHS experimental plots could have favoured its dominance within the Collembola community; research into the effects of increasing available nutrients through fertiliser application has

found evidence that this can alter nematode populations, benifitting different groups (Arancon et al. 2003).

The Collembola found at all sites were *Sminthurinus aureus*, *Friesea* spp., *Isotoma* spp. and *Mesaphorura* spp., in addition to *P. notabilis* which was discussed in Section 3.5.2.1.. Of these *S. aureus* is the only one that represents one taxonomic species although there is considerable variation in pigmentation between individuals and early barcoding work suggests that there are concealed clades (Shaw, pers. comm. 2014). Three species of Friesea were found and two *Isotoma* species, however, the only *Mesaphorura* that was identified was *M. macrochaeta*. As not all specimens were cleared it cannot be said with certainty that this was the only *Mesaphorura* species collected but at least one specimen per sample was cleared and it is known to be a common and widespread species (Hopkin, 2007). It could be that for these common species that the distributions differ at the species level or, as with *P. notabilis*, they represent polyphyletic taxa.

There was dissimilarity in species community composition found between the RHS experimental plots and their adjacent grassland, the data suggests that the RHS experimental plot are essentially flower-beds with the adjacent grassland mirroring the role of the lawn within the garden, this can be seen in the CCA ordination plot (Figure 3.4.5.2.). Some of the differences is species distribution between habitats found here support those previously documented within the literature; *Sphaeridia pumilis* and *Brachystomella* parvula have been found to have a preference for grassland sites by Chauvat et al. (2007).

The plant species richness of the RHS experimental plots was greater than that of the 'plots' at the other sites, but despite this the Collembola diversity was not greater; plant species richness has previously been shown to be positively related to Collembola diversity (Sabais et al. 2011). Again this could be due to a difference in vegetation cover/microclimate. This finding of higher species richness in grasslands than more managed areas is consistent with other studies: Siepel (1996) and Sousa et al., (2006) found that grassland/pastures supported higher Collembola species richnesses than more managed agricultural lands and that low input grasslands had a higher species richness than high input grasslands, respectively. The lower species richness could also be related to the disturbance associated with the management activities, most evidence suggests that disturbance of soil communities leads to loss of diversity (Giller 1996), it is likely that the RHS experimental plots were more disturbed in recent history than the amenity grassland. The total species richness was greater when a vegetation planting treatment (Native, Near native, Exotic) was combined with the adjacent grassland treatment than when combined with another vegetation origin treatment. This is not surprising as it increases habitat heterogeneity, Rumble & Gange (2013), in their work on green roofs also highlight the importance of habitat heterogeneity for supporting microarthropod diversity.

In the adjacent amenity grassland at both the Deer's Farm and the Howard's Field sites *C. thermophilus* was found to be the dominant species. It was the dominant species in soil very similar to that of the Wisley area; an acid sand at Richmond Park, south-west London, (Shaw & Reeve, 2008), situated approximately 20 km to the north-east of the grassland sites used here. The soils of the study sites are all sandy (see Chapter 2., Section 2.1.2.) and *C. thermophilus*, as its name implies, is known to be tolerant of dryer

conditions that are more exposed to heat; it has a more southerly distribution and is locally common in dry disturbed areas (Hopkin & Shaw, 2014). *C. thermophilus* has also been found to be a dominant species at other locations; in the agricultural soils of Higaldo, San Salvador, individuals were collected from rotting tree trunks, debris and beach sand (Castaño-Meneses et al. 2004).

Although no vegetation cover data was collected from the adjacent site it was observed when collecting the soil cores that these plots were 100% covered with vegetation, with no bare ground. So why, when there is more bare ground in the RHS experimental plot, are significantly fewer *C. thermophilus* found there? And why are the densities of *M. minimus* greater?

The relative absence of *C. thermophilus* from the RHS experimental plots is most likely due to differences in vegetation structure. Although there was a higher percentage of bare ground the density of vegetation was greater, for some soil cores it would have created a more sheltered microclimate, the bare patches may not have been large enough to support *C. thermophilus*. Shaw (2003) found it to be an early successional species and Krawczynski (2007) also observed that it was found less frequently and at lower levels at sites with denser vegetation. This species was also absent from Buxton Wood and Wisley Common; trees in the woodland afford shelter and there is a thicker O horizon (see Chapter 2., Sections 2.1.4. and 2.1.5.) and although the heath is more open there is a dense shrub layer of *C. vulgaris*.

Another, less likely, possibility is that the soil of the RHS experimental plots contain metals that were not tested for in the soil analysis. *C. thermophilus* is one of the

Collembola species that has been found to be sensitive to low levels of metal pollution: Fountain (2002) found that *C. thermophilus* were sensitive to increased levels of Zinc; this species was particularly found in soil with a water soluble zinc concentration less than 4938 µg (g^{-1}) being most abundant in soils containing 0-2000 µg (g^{-1}) of water soluble zinc. It should be noted that 4938 µg (g^{-1}) is considerably higher than naturally occurring levels (see Rawlins et al. (2012) for a British survey and Alloway (2008), and references therein, for global levels and concentration risk classifications).

In Chapter 2., Section 2.4.2., it was shown that the soil of the RHS experimental plots at Deer's Farm contained significantly higher concentrations of magnesium. No literature could be found on the effect of magnesium concentrations on *C. thermophilus*, however, as the difference in Collembola density between the RHS experimental plots and their adjacent grassland is more pronounced at Howard's Field where the magnesium concentration was not significantly different, this is unlikely to be the cause.

There is little published research concerning the ecology of *M. minimus*. It is a very small Neelid that is common and widespread, though often overlooked (Hopkin, 2007; Hopkin & Shaw, 2014). It is not a species known to be either acidophilic or acid intolerant being categorised as pH 'indifferent' (Ponge 2000). It has previously been found to be tolerant of the addition of fertilisers at a Scots pine forest in Sweden (Lohm et al., 1977). *M. minimus* densities were significantly greater in the RHS experimental plots than for the adjacent grassland, though this species was still present at relatively high densities in the soils of Wisley Common and Buxton Wood.

The diversity indices calculated for Wisley Common indicate that this was where the greatest Collembola diversity was found. Between October ’11 and April ’13 this was 38 species, more than for all the RHS experimental plots, over the same time period, at either Deer’s Farm or Howard’s Field, despite less sampling effort (soil cores). *F. quadrioculata* ‘group’ was the most abundant species recorded from the soil cores and this has also been observed at other heathland sites (Ponge, Tully, & Gins, 2008; Shaw, 1997). Lowland heaths are designated as a priority for nature conservation due to their stauts as rare and threatened habitats (UK Steering Group 1995) and they are known to be species rich for a variety of flora and fauna communities (Bakker & Berendse 1999). Wisley Common is a lowland heath and already a SSSI and so this has provided additional supporting evidence of its conservation value.

The Collembola species richness of Buxton Wood was less than that of Wisley Common (23 species), using the entire dataset. Previously species richness has been found to decrease along the sequence old forest stand, low input grassland, high input grassland (Siepel 1996). Here in the subset of data for the diversity measures, which were generated from the same number of soil cores, the species richness of the wood was 19 compared to 19 and 13 for the Howard’s Field and Deer’s Farm adjacent grassland sites, respectively (although that of the heath was still greatest: 28 species) (see Table 1. Appendix 3.4.5.), but Buxton Wood may not be the best example of broad-leaved semi-natural woodland.

Buxton Wood was selected because it was a nearby woodland likely to have similar soil properties to the RHS experimental plots and it was chosen to provide a comparison to see what the RHS plots could be if not subject to the impact of Wisley Gardens

horticultural past, however, the ecology of this site will still reflect prior management activities. Previous land-use has been shown to influence the success of habitat recreations (Walker et al. 2004) and relatively speaking this this site has not been a woodland that long, there were very few species indicative of an area that has been a woodland for a substantial period of time, aside from *H. non-scripta*. The length of time since land-use conversion has been found to affect Collembola species richness and community composition (Chauvat et al. 2007; Chauvat et al. 2003). The site is dominated by *B. pendula*, which is typically an early successional trees species, here they are almost planted in rows and although *Q. robur* and *F. sylvatica* were present there were a couple of other trees belonging to species you would not expect to find in natural British woodland: *Pinus nigra* and *Larix decidua*. Although there were few individuals and these were situated the other side of the woodland from the plots, they are unusual and indicate that the site has not been a woodland long and serves as a reminder that it is situated very close to RHS Wisley, although of course this may have nothing to do with how all the trees ended up growing there. The presence of these species was also noted by Phillips and Armitage (2010) in the Wisley Centenary Flora. Buxton Wood is described as an area of woodland that has been extensively planted. Chittenden (1933) refers to the planting of *Castanea sativa*, *L. decidua* and *Corylus avellana* to supply the main garden with poles and stakes, noting the later addition of *F. sylvatica*. Buxton Wood is also the site closest to the M25 (a major motorway encircling London), although shielded, it is less than 150 metres away and it had significantly higher levels of $NO3^-$ though this is not necessarily linked.

3.5.3. Soil fauna diversity: Other taxa

There has been little research on Acari diversity since Petersen and Luxton (1982) noted that few Acari studies identified beyond the order level. In this study over 40,000 Acari were collected and it was not feasible to spend the time identifying these to species level as was accomplished for the Collembola. A recently written identification tool should facilitate this for future researchers (i.e. Shepherd and Crotty (2015)). Previously Acari species have been found to have differing pH preferences (see van Straalen and Verhoef (1997)) and it is likely that different taxa were found at the different sites.

For the other arthropods recorded the abundances were not great enough for meaningful analysis, especially after being split by season, further work could consider these taxa. However, all four of the UK's centipede Orders were represented in the samples, these were mostly Geophilomorpha and predominantly recorded in Buxton Wood and Wisley Common.

3.6. Conclusions

This chapter suggests that although vegetation origin may have had an effect on soil fauna abundances (Acari and Collembola) overall it was not found to have had a significant impact on soil biodiversity (Collembola). This research also suggests that other factors are more important and for maximising soil biodiversity it is suggested to have more than one habitat, for the gardener this could be achieved by simply having both a lawn and a flowerbed; the equivalent of the RHS experimental plots and the adjacent amenity grassland. This chapter also highlights other less direct impacts the incorporation of non-native vegetation could potentially have. This is also one of the few cases where

soil fauna really are influenced by vegetation type with regards to the comparison between the RHS experimental and the non-garden sites.

However, taxonomic diversity is not necessarily the same as phylogenetic diversity, it can be said to not accurately reflect evolutionary histories. The next chapter explores a subset of this data, from the October ’12 samples, using molecular methods.

Chapter 4. Soil fauna phylogenetic diversity

4.1. Introduction

4.1.1. Phylogenetic diversity

This chapter focusses on the effect of vegetation origin on soil fauna biodiversity in terms of the resultant phylogenetic diversity under each vegetation origin treatment. Phylogenetic diversity (PD) is different from taxonomic diversity, as discussed in Chapter 1., Section 1.5.3. (Faith, 1992) and has been suggested as an alternative method for monitoring biodiversity and prioritising conservation efforts (Crozier 1992). Forest et al. (2007) found that areas with the highest taxonomic diversity did not necessarily also contain the highest phylogenetic diversity. That research concerned the flora of South Africa, but the principals are transferable: recently an integrative taxonomic approach, including molecular data, was used to determine the distinctiveness of evolutionary significant units within island bumblebee populations with the aim of guiding conservation policies for conserving genetic biodiversity (Lecocq et al. 2014). For this research to be possible, molecular sequencing work has to be undertaken for the same gene region across the range of taxa studied, this has been facilitated by the DNA barcoding initiative.

4.1.2. Barcodes for life

DNA barcoding has been suggested as a method of alleviating the taxonomic impediment to the study of soil fauna (Rougerie et al. 2009). It was Hebert et al. (2003) who proposed that a region of the cytochrome oxidase 1 gene could be used as a taxonomic tool to barcode all known animal species for identification purposes and help correctly place those newly discovered. The cytochrome oxidase 1 gene, also known as the COI, CO1 or

COX1 region, is a 650 base pair fragment found on the mitochondrial genome. It is now approved by the Consortium for the Barcode of Life (CBOL) as the default barcode region for use in the animal kingdom (Hanner 2012). The plant equivalents are rbcL and matk (Fazekas et al., 2012; Jeanso, Labat, & Little, 2011) found on the chloroplast genome, with the ITS region approved for Fungi (Schoch et al. 2012)).

There are over 57,000 (57,250 on 18/6/15) Collembola DNA sequences on the barcode of life data system: BOLD (Ratnasingham & Hebert 2007); a repository for DNA barcode sequences. BOLD is interlinked with the partner organisation GenBank; a public DNA sequence database managed by the National Center for Biotechnology Information: NCBI (Mizrachi 2007). These BOLD sequences are for the COI region, but only approximately 5,500 have been identified to species level and these only cover 518 of the estimated 6,500 - c 7,000 described species of Collembola found worldwide (Hopkin 1997; Deharveng 2004) (as of 18/6/15). For other arthropod groups coverage is more complete (e.g. the Lepidoptera, see Hebert, deWaard and Landry (2010)). The barcoding of this region has enabled researchers to identify Collembola to species from the gut content analysis of animals that prey on them (Agustí et al. 2003).

The 18S ribosomal DNA region was developed by the Blaxter Nematode Genetics Lab as an identification tool for nematodes (Blaxter et al. 2000) and is effective in discriminating between protist lineages (Pawlowski et al. 2012), though it is not currently authorised for use as a barcode by CBOL. It uses the small subunit 18S gene which codes for a component of the ribosome in eukaryotes. Problems have been reported for this region as a universal molecular barcode: it doesn't cover all taxa (e.g. in the Phyllum Mollusca (Meyer et al., 2010)), there are difficulties in establishing primary homology (Shull, et al.,

2001; Wilson, 2010) which results in problems during sequence alignment and it may not accurately reflect true diversity (Tang et al. 2012). However, there are records for Collembolan 18S sequences on GenBank and primers for this region have been used to successfully identify Collembola within the gut contents of other arthropods (Kuusk & Agustí 2008).

4.1.3. Collembola barcoding, phylogenetic species delimitation and diversity

As the Collembola were the aspect of soil fauna for which diversity at the species level was compared in Chapter 3., for the same reasons discussed in Chapter 1. Section 1.3.2., and to enable a comparison between taxonomic and phylogenetic diversity, they were the group selected to be the focus of the molecular phylogenetics work.

When researching soil fauna biodiversity, the Collembola have previously been targeted for analysis due to their numerical dominance within the soil ecosystem compared to other soil arthropods (Petersen & Luxton 1982; Hogg & Hebert 2004), however, despite this there is an acknowledged taxonomic impediment hindering their study (André et al. 2002; Rougerie et al. 2009). The need for an approach to Collembola systematics that combines traditional morphological character based taxonomy and molecular taxonomy has been recognised (Deharveng 2004). Molecular work can be used to uncover new characters to aid in species classification and identification (Regier et al. 2010). The first step to this still requires that Collembola be collected and described/identified.

Hopkin (2007) estimated the number of Collembola species present in the UK to be around 250 species with the national recorder estimating that there are probably closer to 381 spp. in 2015 (Peter Shaw, pers. comm., 2015). The full British and Irish checklist in

Hopkin (2007) extends to 383 species, although many of these records are annotated as being doubtfully present; those for which there are definite records (unequivocal literature records or specimens) add up to 247 species (Hopkin, 2007). Currently of these 247 recognised UK Collembola species, 86 have DNA sequences available on GenBank with 63 of these having been sequenced for the COI barcode region and the remaining 23 for other regions (28S, 12S, COII, cytb). Only a fraction of these specimens also have associated voucher images on BOLD (figures from June 2015). This means that compared to the sequencing efforts in some other taxonomic groups for larger geographic areas, e.g. the Lepidoptera of the eastern half of North America where coverage for the COI region was 99.3% in 2010 (Hebert et al. 2010), the current figure of 25.5% coverage for the UK Collembola is relatively low.

There is uncertainty in this molecular deficit figure, in actual fact it could be greater. The most recent version of the UK Collembola key (Hopkin, 2007) did not include all the species present; some were omitted (e.g. *Heteromurus major*), the status of other species now known to definitely be present (e.g. *Dicyrtomina saundersi* (Hopkin & Shaw, 2013a)) was unclear in 2007 and for other species delimitation decisions have yet to be finalised (e.g. *Sminthurinus reticulatus* (Hopkin & Shaw, 2014)), whilst others remain unclear (e.g. *Protaphorura* spp. (Shaw et al. 2013)).

Molecular data have been used to aid in species boundary clarification though species delimitation issues have arisen as a result of molecular work even within well characterised and widespread Collembola, such as *Parisotoma notabilis* (see also Chapter 1. Section 1.5.4.). This species has a Nearctic to Western Palearctic distribution and is '*probably present in every hectad in UK/Eire*' (Hopkin & Shaw, 2013). Prior to the work by

Porco et al. (2012) it was considered a singular, readily identifiable species with homogenous, distinctive morphological characters. However, based on DNA sequences from the COI standard barcode region it was proposed that *P. notabilis* is actually comprised of at least four lineages (L0, L1, L2, L3) with a clear geographical pattern, with L0 determined as the lineage present in the UK, although Porco et al. (2012) only used one specimen collected from Hampshire for the study. This molecular work produced phylogenetic trees with a polyphyletic *P. notabilis*; other described *Parisotoma* species fell between the *P. notabilis* lineages. Within systematics, monophyly has been increasingly used as a criterion to set species boundaries, based on the phylogenetic species concept and this has knock on implications for comparisons of biodiversity and conservation effort prioritisation (see Agapow et al. (2004)). From the research by Porco et al. (2012) it is not possible to say with confidence that *P. notabilis* L0 is the only lineage present in the UK, but there is strong evidence that this species group needs revision.

In addition to exploring specific taxa relationships, molecular genetic data has other applications. Collembola DNA sequence data has been used to explore species biogeography patterns, see Shaw, Faria, and Emerson (2013) for a review of recent advances in this field. Patterns of phylogeography can be examined when phylogenetic and species distribution data are combined (e.g. Cicconardi et al. (2009); Emerson and Gillespie (2008)) whilst phylogenies have been incorporated into the study of soil community ecology (Emerson et al., 2011). High throughput sequencing platforms e.g. the Roche/454 FLX (Margulies et al. 2005), see Mardis (2008) for other next-generation sequencing platforms), have facilitated the sampling of whole communities. This has been achieved for marine meiofauna communities (Fonseca et al. 2010; Creer et al. 2010) and tropical rainforest communities (Creer et al. 2010) both of which contain invertebrate

species diversity and it is a technique now being applied to Collembola and soil communities (Shaw et al. 2013). It does have the drawback that specimens cannot be re-examined in light of the sequence data (no voucher specimens/photographs) and unless a barcode is already available for the species sequenced identification is not possible. There is currently a soil research initiative that includes the barcoding of Collembola in its remit and should add to the pool of available barcode sequences on BOLD, but for now it is limited to grassland habitats (Natural England 2015).

With greater Collembola barcode region coverage it will be possible to conduct phylogenetic analysis without undertaking molecular sequencing by downloading sequences from GenBank or BOLD, however this kind of approach should not be taken without caution. It relies on the taxonomic expertise of the specimen collector, the quality of the sequence (you are unable to see the trace files) and that errors were not made in uploading selection process.

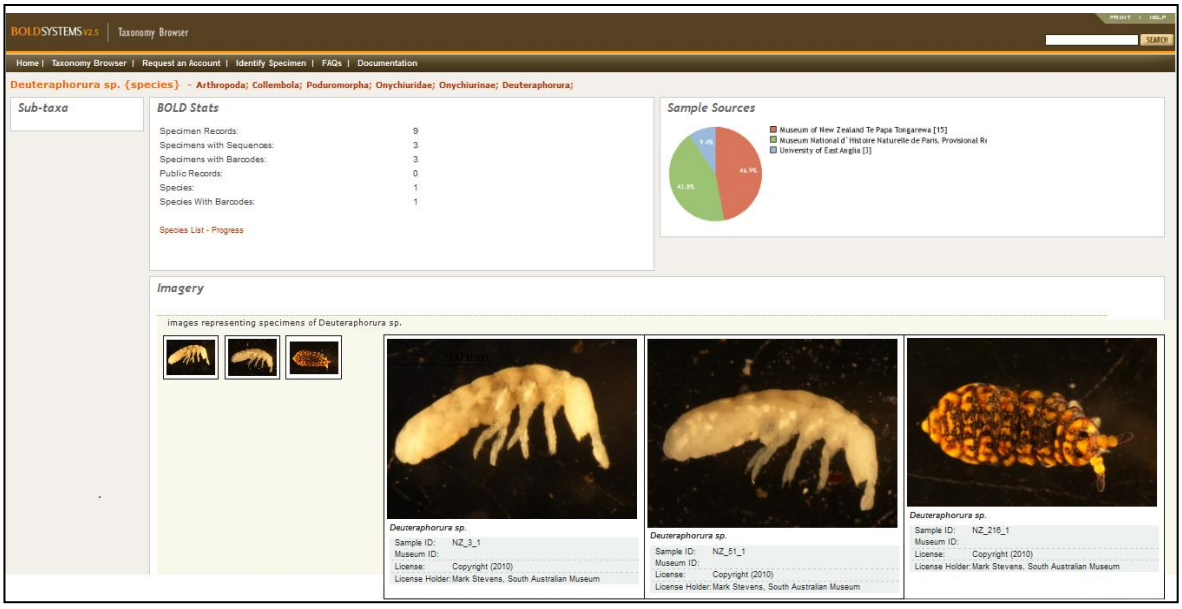

Figure 4.1. Three *Deuteraphorura* species records available on BOLD (January 2013 (URL no-longer available as it has since been corrected and the website updated)).

The incorporation of photographs serving as voucher specimens does go some way to ameliorating this, see Figure 4.1., this is the most apparent of several specimen misidentifications/upload errors encountered during the molecular work (thankfully now rectified).

This molecular work explores the Collembola community structure and its phylogenetic diversity (PD), using the COI region of the mitochondrial genome. It includes the sequencing of Collembola for which there are currently no available sequences on BOLD (25 species). The phylogenetic diversity between the RHS experimental plot vegetation origin treatments (Native, Near native, Exotic) is compared and that of the different habitats is explored and discussed. As there was no difference in taxonomic diversity between the different vegetation origin treatments in terms indices measured (H' and 1-D (Chapter 3., Table 3.4.4.1., Section 3.4.4. and Chapter 3., Section 3.5.2.1.)), the phylogenetic analysis was conducted with the null hypothesis (H0): all the Collembola PD values belong to the same population and the alternative hypothesis (Ha): at least one of the vegetation origin treatments does not belong to the same population (the PD of the Collembola from that treatment is significantly greater or less than expected).

4.2. Methods

The molecular work was undertaken at the University of Reading (January '13 - April '13). The Collembola processed for this were retrieved from the soil cores collected during the October 2012 sampling occasion and extracted into 100% molecular biology grade ethanol, see Chapter 3., Section 3.2.1.. This has been found to be a suitable method of sample preservation used by other studies for similar work (e.g. Hogg and Hebert (2004)). The Collembola found were initially grouped and identified according to Chapter 3.

Section 3.2.2.; for the pooled species groups; *Friesea* spp., *Mesaphorura* spp. and *P. armata* 'group', *F. quadrioculata* 'group', the specimens used for the molecular work were then identified to species using Hopkin (2007). All of the *Isotoma* spp. samples were identified as *I. anglicana*. Where possible, several individuals representing each species were taken in case the first extractions proved unsuccessful, however, for eleven of the required taxa only one specimen was available. See Table 1. Appendix 4.2. for a list of the Collembola species retrieved in the October '12 sampling; the number of specimens available for each species from all sites and just the RHS experimental plots and the site/treatment the individual used came from. For the comparison between the vegetation origin treatments, specimens to represent the species were preferentially selected as those originating from the RHS experimental plots. In some cases although damaged specimens were still identifiable, they were not considered ideal for molecular work purposes and where the required taxa were also present at other sites these samples were then used if in a better condition (to minimise repeat extractions).

The aim was to obtain at least one sequence for each species present at the RHS experimental sites with additional sampling within the Symphypleona so that the unknown Katiannida species (Chapter 3., Section 3.4.4. and Figure 3.4.4.6.) could be placed with greater confidence and to aid in resolution of the *Sminthurinus reticulatus*/*S. elegans* relationship, where there is debate as to whether the former is a valid species or represents a colour form of the latter (Hopkin & Shaw, 2014). Across all sites seven *P. notabilis* samples were processed for molecular work to determine with greater confidence which lineages (see Porco et al. (2012)) were present if time permitted.

4.2.1. DNA extraction

DNA was extracted using a Qiagen DNeasy kit (supplied by QIAGEN). Research focussing on Collembola and other small arthropods have used this method to obtain total DNA from specimens (Luan et al. 2005; Schneider et al. 2011; Timmermans et al. 2010; Yang et al. 2014; Kuusk & Agustí 2008). The required region is found in the mitochondrial genome so there are often high levels present in the muscular tissue of arthropod legs. Levels of mitochondria in Collembola legs have been found to be insufficient as some species are too small. Timmermans et al., (2010) were able to use partial specimens depending on the size of the insect (Coleoptera preserved in 100% ethanol: mitochondrial barcoding region), however, Rougerie et al., (2009) found it necessary to extract DNA from whole specimens of Colembolla, as did Schneider, Cruaud, and D'Haese (2011) who worked on the phylogenetics of the Neelipleona, the order to which *Megalothorax minimus*, the smallest Collembola retrieved in this study, belongs.

A low cost Chelex-based method was trialled, see Ivanova et al., (2009). Chelex has been used to successfully extract DNA from arthropods; Casquet, Thebaud, and Gillespie (2011) used a 10% Chelex solution with Proteinase K to extract DNA from the legs of *Argyrodes* spiders. Although species of this genus are small, their legs are still larger than whole individuals of some of the Collembola species retrieved from the soil cores in this study, this method did not result in reliable Collembola DNA extraction. SDS/CTAB methods have been found to yield greater less degraded DNA quantities (Chen et al., 2010), however, due to time constraints these were not tested as they are more laborious.

As the entire specimen was used per extraction, all specimens were photographed prior to DNA extraction, to serve in place of a voucher, with determining features visible where

possible. A digital camera (QImaging QICAM Fast 1394) was used, attached to either a dissecting microscope (Olympus SZX16) or a high power compound microscope (Olympus BX50), see Figure 4.2. for examples. These will be uploaded to the Barcode of Life Data System with their associated sequences.

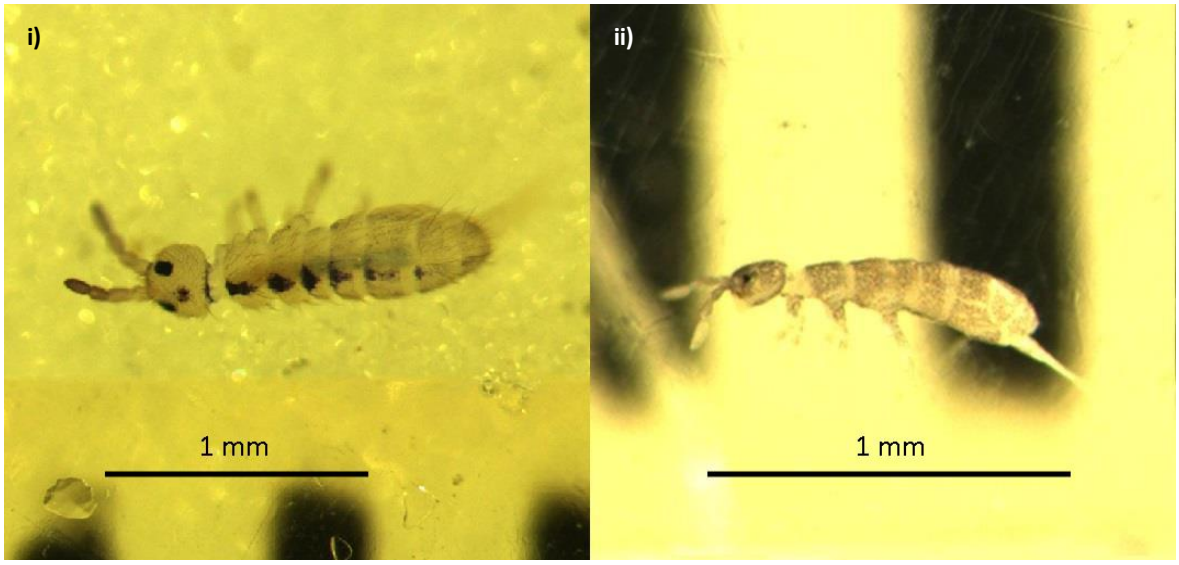

Figure 4.2. Voucher photographs: i) *Isotomurus palustris* (plot H4) and (ii) *Parisotoma notabilis* (plot H1ZA), scale included in mm.

The QIAGEN DNeasy supplementary protocol (Qiagen 2006) was followed with modifications: using a dissecting microscope the specimens were broken against the side of the microcentrifuge tubes using autoclaved pipette tips (step 2) and DNA was eluted with 20 µl Buffer AE to increase the final DNA concentration (step 8). To create a set of back-ups step 9 was followed; again DNA was eluted with 20 µl Buffer AE. Each set of extractions were run with both a negative and a positive control, to ensure any possible contaminations of stock solution were spotted and to facilitate trouble shooting where extractions failed, respectively.

Total DNA extractions were run on an agarose gel in an effort to determine the DNA concentration and to inform decisions on the initial volume of total DNA to include in

polymerase chain reactions (PCR). Gels were made using 1.5 g agarose dissolved in 100 ml buffer (1x TAE) and 3 µl (10 mg/ml) ethidium bromide, loaded with samples, dye and a ladder, run for approximately 1.5 hours at 90 - 100 V, then viewed using a gel imager (BioDoc-It Imaging System). However, the concentrations of total DNA extracted were too low to visualise, so spectrophotometer (Thermo Scientific NanoDrop Lite) readings were used to determine DNA concentration and gauge the amount of total DNA to add to the PCR reactions. The NanoDrop machine was blanked with the Buffer AE from the DNeasy kit and per sample 1 µl of total DNA was pipetted onto the detector lens.

4.2.2. DNA amplification and sequencing

The COI 'barcode' region (see Hebert et al. (2003)) of the mitochondrial genome was chosen for amplification, by PCR, because of the widespread use of this region within the literature and of the availability of primers (e.g. Folmer et al. (1994)). This aligns with the research goals set out by Natural England (research project 1439 (Natural England 2015)). The base sequences for the primers used: ColFolmer-for (forwards) and ColFolmer-rev (reverse) were supplied by Brent Emerson (based at the Instituto de Productos Naturales y Agrobiología) who recommended them as effective for Collembola. The primers were ordered from Sigma-Aldrich and diluted to obtain the required stock solution concentrations, see Table 2. Appendix 4.2. for the primer sequences.

Reactions were carried out in 25 µl volumes: 12.5 µl BIOMIX, 1 µl (0.447 µM) forwards primer, 1 µl (0.321 µM) reverse primer, DNA (1 - 2.5 µl dependent on quality) and made up to the total reaction volume of 25 µl with nanopure water (8 - 11.5 µl) (obtained from a Milli-Q Direct 8 Water Purification System).

The PCR profile used was run on an Applied Biosystems GeneAmp PCR system. The programme used was a combination of that recommended by Brent Emerson (Emerson, pers. comm., 2012) and that used by Schneider, Cruaud, and D'Haese (2011) who worked on the phylogenetics of the Neelipleona. It used the temperatures and timings suggested by Emerson, but with the adaption of five starter cycles. It consisted of an initial denaturing step at 95 °C for 2 mins, 5 amplification cycles (95 °C for 1 min, 50 °C for 45 secs, 72 °C for 1 min), followed by 35 cycles with an annealing temperature of 52 °C (so: 95 °C for 1 min, 52 °C for 45 secs, 72 °C for 1 min) and a final step at 72 °C for 5 mins.

PCR products were run on a gel, made to the same specifications as in Section 4.2.1. but run for an hour at 90 V to check for successful amplification, with a negative control and alongside a 100 base pair ladder. Where bands were not observed, DNA was re-extracted from another specimen of the required species and where bands were faint PCR was attempted again with an increased total DNA component volume. PCR products were stored frozen (-20 °C) until enough had accumulated to be processed for sequencing.

Successful PCR products were purified using QIAquick PCR purification kits (QIAGEN) and sent to Source BioScience (Oxford laboratories) for Sanger sequencing in both directions with the forwards and reverse primers.

4.3. Analysis

4.3.1. Phylogenetic tree construction

The COI sequences were assembled; consensus sequences built from the forwards and reverse sequencing in Seqman Pro (DNASTAR). Sequences were 'blast searched' on GenBank to check that they fell within the right area (ensures that instances where non-

target DNA has been amplified are caught and that the correct sequences were returned from the sequencing laboratories). For the taxa it was not possible to obtain sequences for, where available, these were downloaded (FASTA format) from GenBank and BOLD, see Table 1. Appendix 4.3. for accession numbers and collection details. Sequence selection was made based on the following criteria: voucher image availability, sequence from reliable/published source and sequence quality (few or no ambiguity codes). This was not necessary for the tree built from the RHS experimental plot vegetation origin treatment data as a sequence was retrieved for each Collembola species present. Any repercussions this could have had for the phylogenetic tree construction for the Collembola species from all sites is fully discussed in Section 4.5.2.. All sequences were then aligned in Bioedit using the ClustalW multiple alignment tool. The alignment was manually optimised with sequence read ends being trimmed where necessary to remove primers.

The sequence data was used to build phylogenetic trees of the relationships between Collembola species found in the assemblages of each plot, nested within a tree containing all the species retrieved from the October '12 sampling of the RHS experimental plots. A Protura sequence (*Andinentulus rapoporti* (Condé 1963)) was selected as an outgroup: GenBank accession number: KJ395313. Although molecular and morphological phylogenies do not always agree on the relationship between the basal hexapods (Carapelli et al. 2000; Carapelli et al. 2006; Grimaldi 2010) with some molecular research placing Diplura and Protura together, excluding Collembola (e.g. Giribet et al. (2004) and Luan et al. (2005)) but with the morphological data based consensus consistently placing the Protura as a sister group to the Collembola (Hennig 1965; Kukalová-Peck 1983; Luan et al. 2005). Most recently Misof et al. (2014) found branch support values over 98% for

Protura and Collembola being most closely related in a multi-gene molecular analysis, so this is the logical choice for an outgroup. Even if Diplura are more closely related to the Collembola this does not present a problem; there is strong evidence from the research above that both Collembola and Protura are monophyletic, all that is required of an outgroup is that it does not fall within the taxon explored and is also not too distantly related either; Schneider et al. (2011) used Thysanura, Archaeognatha and Decapoda outgroups. The Protura sequence used here was selected as it did not contain any ambiguity codes and the sequence could be traced to published peer reviewed research (Shrubovych et al. 2014); no Protura sequences were associated with images on BOLD.

To build preliminary phylogenetic trees the alignments were uploaded to the Cyberinfrastructure for Phylogenic Research (CIPRES) Portal (Miller et al. 2010) and RAxML (Randomized Axelerated Maximum Likelihood) version 3.1 (Stamatakis et al. 2008) was used to construct maximum likelihood phylogenetic trees with branch lengths.

To obtain phylogenetic trees with improved branch support values, MrModeltest version 2.2 (Nylander 2004) was used to select the best base substitution model out of the range that could be implemented by MrBayes (Ronquist et al. 2012), in PAUP* (Swofford 2003). PAUP* requires files in a NEXUS format, for this files were converted in Mesquite (Maddison & Maddison 2006). It was not necessary to code gaps in the alignment as there were no indels visible (insertion deletion events that result in alignment gaps). For both the RHS experimental plot vegetation origin treatment analysis and for the phylogenetic tree covering all sites the base substitution model: GTR + I + G (general time reversible 'GTR' model with a proportion of invariable sites 'I' and gamma distributed rate variation among sites 'G') was selected based on AIC scores; this model had the lowest

value scores. The hLRT scores also indicated that this was best fitting model (GTR + I + G has previously been found to be the best fitting model for other protein coding mitochondrial genes for a range of Coleoptera (Timmermans et al. 2010)).

The GTR + I + G model was implemented in MrBayes version 3.2.3 (this uses Bayesian inference: Markov chain Monte Carlo (MCMC) methods to build phylogenetic trees) via the CIPRES Science Gateway version 3.3, see Appendix 4.3. for the MrBayes code block. The output file for the consensus tree was produced in a NEXUS format with the branch lengths and support values for each branch, however, for further analysis conversion to a Newick format was required. The NEXUS files were opened using FigTree version 1.3.1 (Rambaut 2009) and exported in a Newick format with the branch length values.

4.3.2. Phylocom phylogenetic diversity analysis

The phylogenetic consensus tree for the RHS experimental plot Collembola, from the analysis in MrBayes, was processed in Phylocom version 4.2 (Webb, Ackerley, & Kembel, 2008). The Newick string was read alongside a file designating clumps for analysis, see Table 2. Appendix 4.3. for the 'sample' file specifying the clumps. A total of 35 clumps were specified; one for each of the plots subject to the different vegetation origin treatments (no Collembola were retrieved from plot H6EA for October '12, so this clump did not need to be specified and the corresponding values were set to 0). Phylocom was used to calculate phylogenetic distance matrices between taxa (using the branch lengths) within the specified clumps and generate community structure metrics, for each plot, for analysis (see Webb et al. (2008) and the Phylocom manual, Webb et al. (2011). The presence and abundances of the mangled specimens not identified to the species level

were excluded from the phylogenetic diversity analysis (less than 1% of specimens, see Table 3., Appendix 4.3. for plot treatment origin).

The command 'pd' was used to calculate the phylogenetic distance; the total branch length between all the taxa found in each plot known as Faith's Index of phylogenetic diversity (PD) (Faith 1992). The command 'comstruct' was used to calculate the mean phylogenetic distance (MPD), the average distance (branch lengths) between two randomly drawn individuals drawn from each plot (999 random draws), see Webb et al., (2008). MPD incorporates the abundance of each taxon into the analysis. For both these measures of phylogenetic diversity, PD and MPD, treatments with a greater phylogenetic diversity would be expected to have correspondingly greater scores. Communities which are more closely related or where one species is dominates a sample would have a lower MPD score than a more phylogenetically diverse or evenly distributed community.

To determine any statistically significant differences in the phylogenetic diversity of the Collembolan community structures between the different treatments, two-way ANOVAs were performed in R for both the PD and MPD metrics, separately, after the data were found to be normally distributed for PD (Shapiro-Wilk: $p = 0.8$). The MPD scores were not normally distributed (Shapiro-Wilk: $p = 0.02$), however as the sample size was small ANOVA was considered the most appropriate test. The hypotheses stated at the end of Section 4.1.3. were used, with 'site' (Deer's Farm or Howard's Field) and the vegetation origin 'treatment' (Native, Near native and Exotic) set as factors. This analysis was conducted in Rstudio (RStudio, 2014), version "Spring Dance" using the R core package 'stats' (Chambers & Hastie 1992).

A Pearson's correlation coefficient was calculated to assess the relationship between the phylogenetic diversity scores of each RHS experimental plot and the corresponding species richness (R), with the null hypothesis (H0): the PD values are positively correlated with R, and the alternative hypothesis (Ha): there is no correlation between PD and R. Species richness is the simplest measure of taxonomic diversity (see Chapter 1., Section 1.5.2. for explanation and Chapter 3. Section 3.4.4. for results for all sampling occasions). Both these calculations excluded the ten specimens where it was not possible to identify the individuals to species level.

4.4. Results

In total, across all sites, successful COI sequences were obtained for 45 Collembola species. For eleven species more than one individual was sequenced, see Table 1., Appendix 4.4. for the number of sequences obtained per species. For 25 of these species COI sequences were not already available on GenBank, as of June 2015, and for 20 of these species no gene regions were available, see Table 1., Appendix 4.4..

Extractions were unsuccessful for *Schoetella ununguiculata* and as there was only one individual of this species it was not possible to re-extract. This was also the case for *Entomobrya marginata* and *Bourletiella arvalis*; where only one specimen was available, and for *Sminthurides schoetti* where only two individuals were collected with neither amplifying successfully during PCR. In total it was not possible to retrieve COI sequences from four species: see Table 1. Appendix 4.2. for coverage of the molecular work. However, sequences for *E. marginata* and *S. ununguiculata* were available to be downloaded from GenBank/BOLD. See Table 1., Appendix 4.3., for the collection details of

the additional sequences. It was not necessary to download additional sequences for the construction of the phylogenetic tree for the RHS experimental plots.

Phylograms of the consensus trees built using the Collembola COI sequences, with branch support values, are shown in Figure 4.4. (RHS experimental plots) and Figure 4.4.4. (all sites).

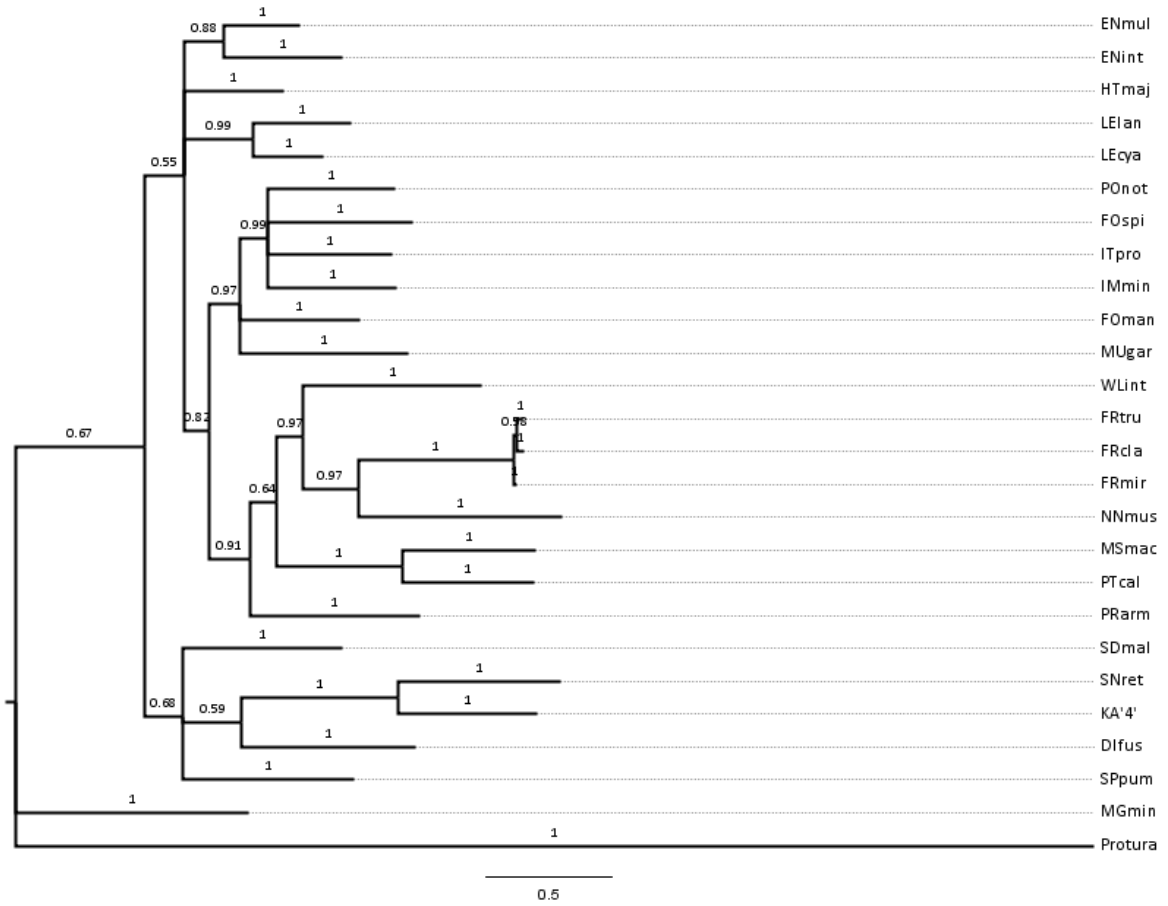

Figure 4.4. Phylogram of the consensus tree for the Collembola species retrieved from the RHS experimental plot soil cores collected October '12, with clade probability values indicated above branches and a Protura sequence set as the outgroup (drawn in FigTree version 1.3.1.). See Appendix 3.4.2., Table 2., for interpretation of species codes.

4.4.1. RHS experimental plots: Phylogenetic diversity

Phylogenetic diversity was calculated using the branch lengths of the consensus tree shown in Figure 4.4.. A two-way ANOVA test found no significant difference in PD between either the the vegetation origin treatments ($F_{2, 30} = 2.888$, $p > 0.05$) or the two RHS experimental sites ($F_{1, 30} = 0.002$, $p > 0.05$), although the interaction between 'site'

and 'treatment' was significant ($F_{2, 30} = 3.984$, $p < 0.05$). H0 was accepted, see Figure 4.4.1. for a graphical representation of the PD of the RHS experimental sites separated by vegetation origin treatment. See Appendix 4.4., Table 2. and Figure 1. for the full two-way ANOVA results including interaction terms and the plots of the residuals, respectively.

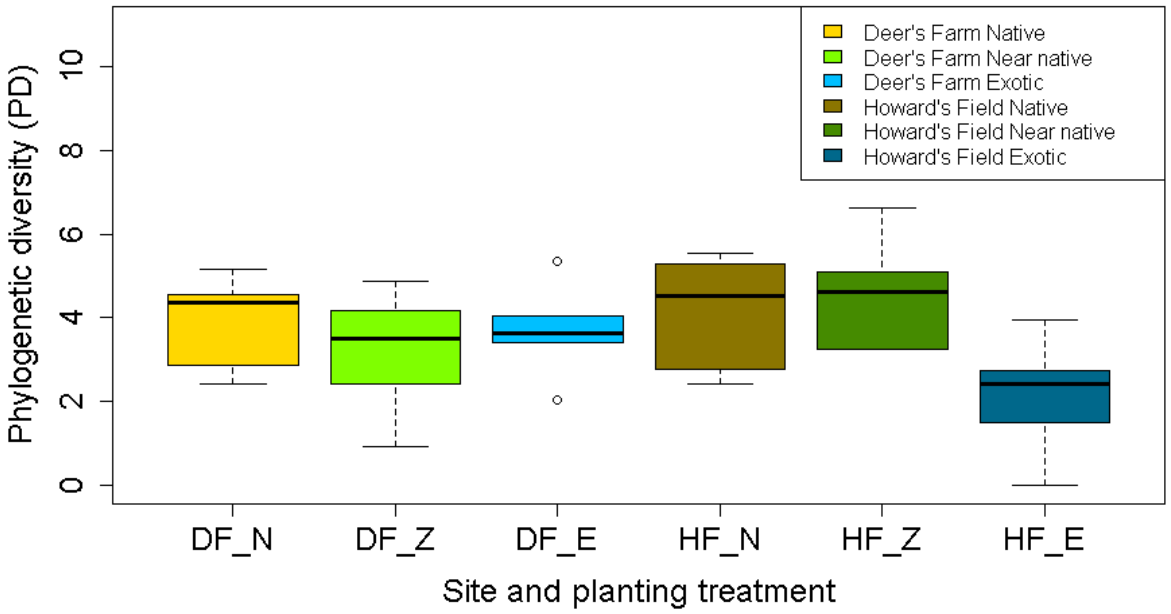

Figure 4.4.1. Boxplots of phylogenetic diversity for the RHS experimental plots at the Deer's Farm site (DF: lighter left hand tones) and the Howard's Field site (HF: darker right hand tones). Native (N): yellow, Near native (Z): green, and Exotic (E): blue.

4.4.2. RHS experimental plots: Mean phylogenetic distance

Mean phylogenetic distance was calculated using the branch lengths of the consensus tree shown in Figure 4.4.. A two-way ANOVA test found no significant difference in MPD between either the the vegetation origin treatments ($F_{2, 30} = 1.066$, $p > 0.05$) or the two RHS experimental sites ($F_{1, 30} = 2.375$, $p > 0.05$) or the interaction term ($F_{2, 30} = 0.019$, $p > 0.05$). H0 was accepted, see Figure 4.4.2. for a graphical representation of the MPD of the RHS experimental sites separated by vegetation origin treatment. See Appendix 4.4., Table 2. and Figure 2. for the full two-way ANOVA results including interaction terms and the plots of the residuals, respectively.

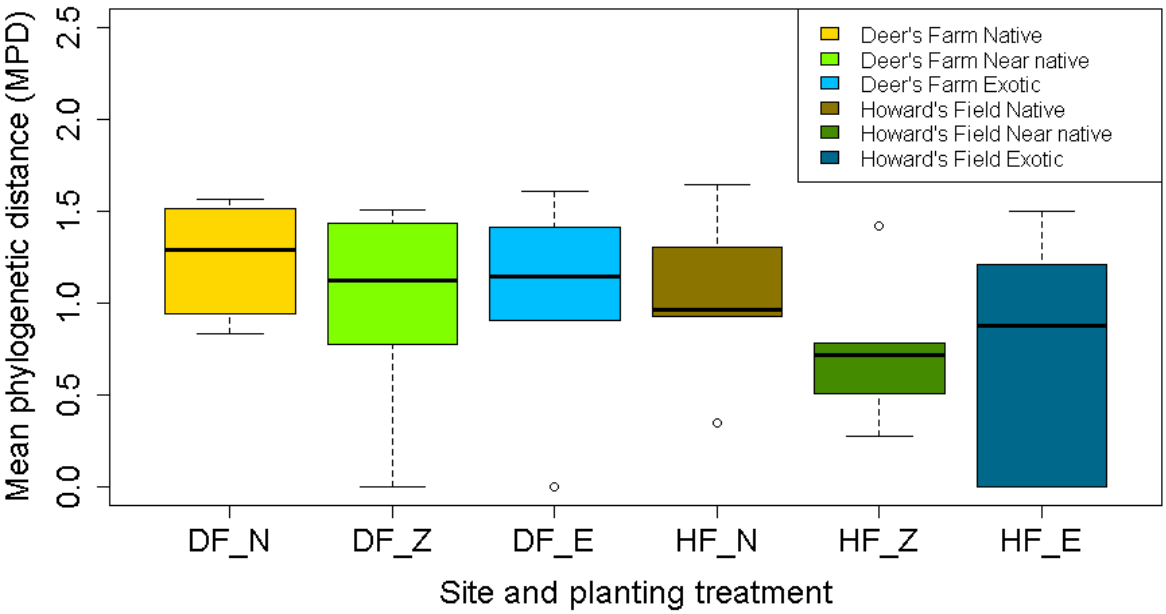

Figure 4.4.2. Boxplots of mean phylogenetic distance for the RHS experimental plots at the Deer's Farm site (DF: lighter left hand tones) and the Howard's Field site (HF: darker right hand tones). Native (N): yellow, Near native (Z): green, and Exotic (E): blue.

4.4.3. RHS experimental plots: Phylogenetic diversity comparison to taxonomic diversity

A Pearson correlation coefficient was calculated to assess the relationship between PD and species richness for the RHS experimental plots; there was a strong positive correlation between the two parameters ($r = 0.96$, $n = 36$, $p < 0.001$), see Figure 4.4.3. below.

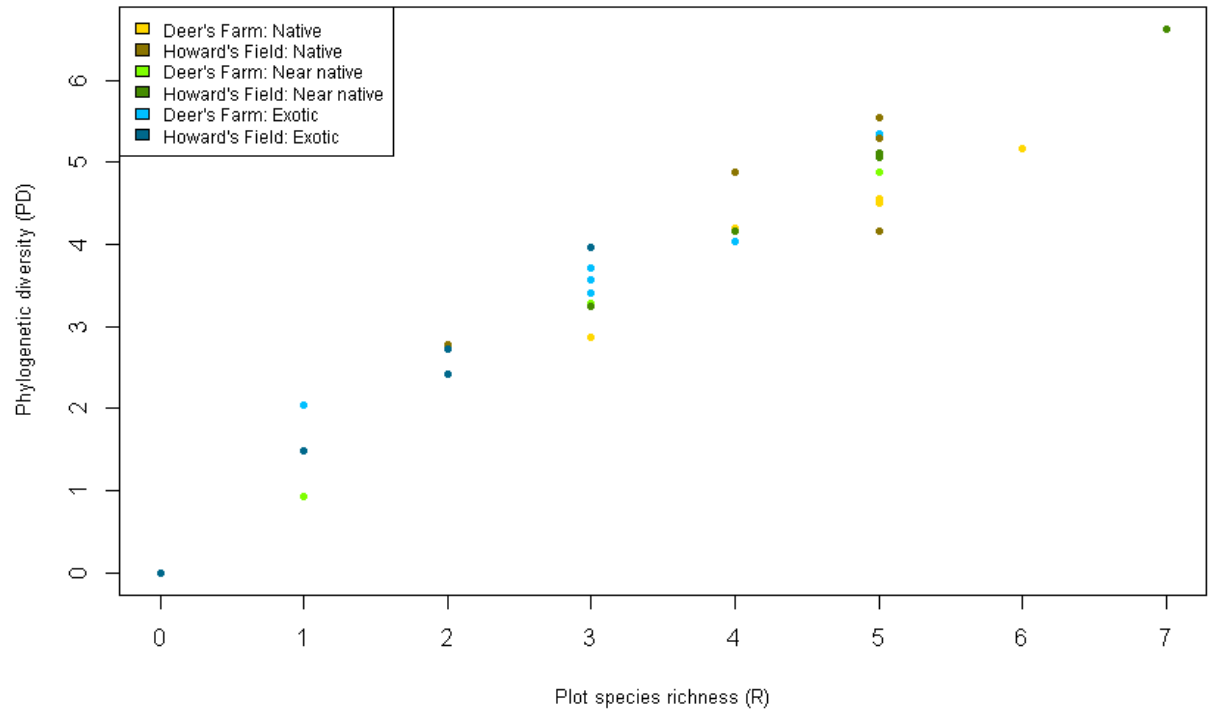

Figure 4.4.3. Scatter plot of PD and R values for the RHS experimental plots (October '12).

4.4.4. All sites: Phylogenetic diversity

A phylogeny was constructed from all the COI sequences collected for this research; 59 sequences from 45 species, with two additional sequences downloaded from GenBank/BOLD (see Section 4.4.). Two species are not represented: *Bourletiella arvalis* and *Sminthurides schoetti*, from the Deer's Farm adjacent grassland site and Wisley Common, respectively. See Figure 4.4.4. for a phylogram of the consensus tree with the species marked according to site occurrence. It was possible to include more than one sequence for the following species: *Parisotoma notabilis*, *Lepidocyrtus lignorum*, *Lepidocyrtus cyaneus*, *Protaphorura armata*, *Mesaphorura macrochaeta*, *Sminthurides malmgreni*, *Dicyrtoma fusca* and *Sminthurinus elegans*.

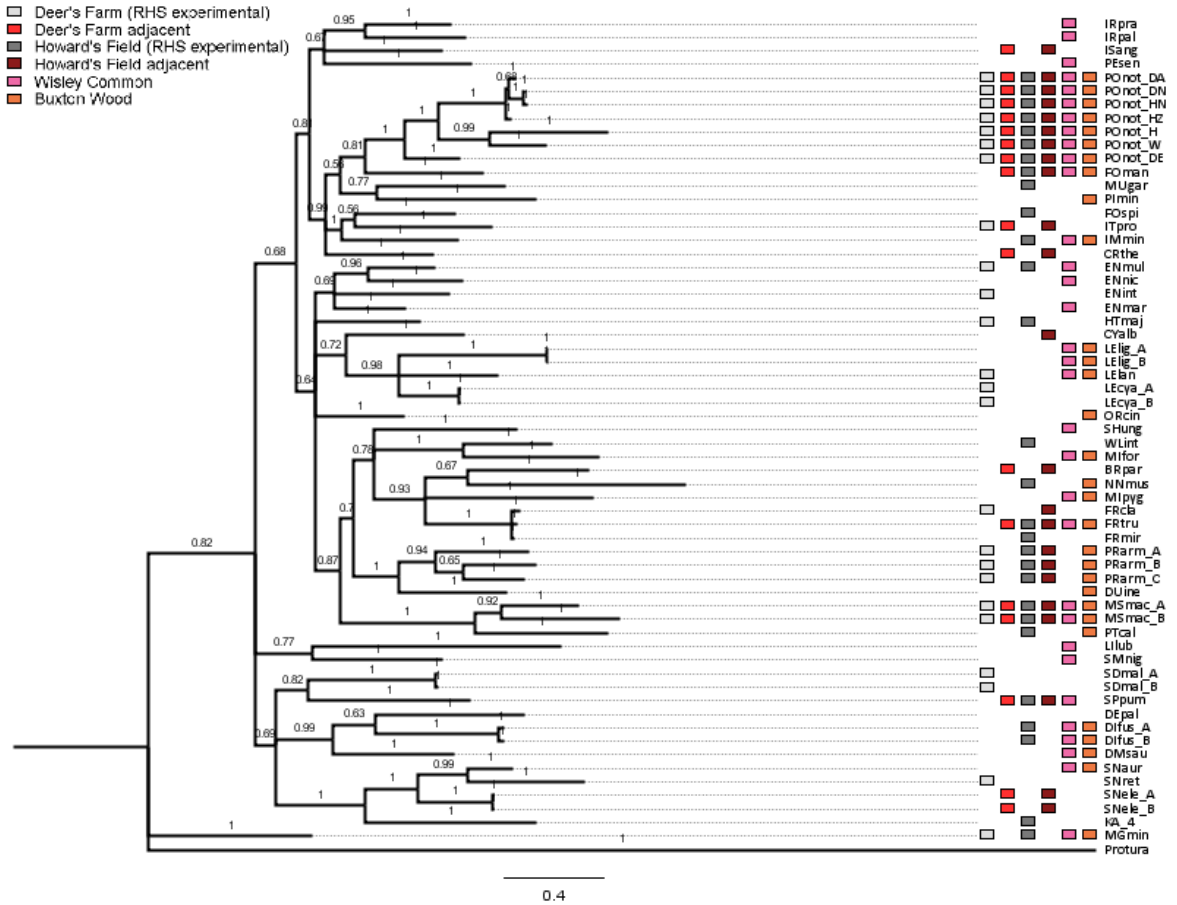

Figure 4.4.4. Phylogram of the consensus tree for the Collembola species retrieved from all soil cores processed from the October '12 sampling, with clade probability values indicated above branches and a Protura sequence set as the outgroup (drawn in FigTree version 1.3.1). See Appendix 3.4.2., Table 2., for interpretation of species codes. Filled squares to the left of the species code indicate which site(s) the species occurred at.

4.5. Discussion

4.5.1. Phylogenetic diversity: RHS experimental plots

For the RHS experimental plots there was no statistically significant difference in phylogenetic diversity between the different vegetation origin treatments. This means that the lengths of the evolutionary pathways connecting the species present under each of the treatments do not differ, they encompass a similar range of genetic diversity which supports the hypothesis that vegetation origin does not affect soil biodiversity. There was no significant difference in phylogenetic diversity between the two RHS experimental sites, although the interaction effect between site and treatment was significant (when the interaction was removed and the 2-way ANOVA repeated, site and treatment remained non significant (see Table 3. Appendix 4.4.).

No significant difference in mean phylogenetic distance (MPD), which is sensitive to relative abundances of taxa, was found between the Collembola communities of the different vegetation origin treatments. This suggests that the communities found cover similar ranges of phylogenetic diversity. The MPD metric enabled the reincorporation of measures of species evenness and dominance concentration into the phylogenetic diversity comparison (assessed taxonomically by the H' and 1-D indices).

In Chapter 3. no differences in the diversity indices calculated for the Collembola were found between the vegetation origin treatments of the RHS experimental plots. However, the Kruskal-Wallis tests conducted per species found that there were differences in species abundance across the vegetation origin treatments for three species out of the 44 found for all sampling occasions (but analysed per season, see Chapter 3., Table 3.4.4.2.). For the Chapter 3. autumn analysis which included the October '12 data set used in this

molecular work, two species were found to have differences in distribution between the treatments: *Heteromurus major* and *Sphaeridia pumilis* (see Appendix 3.4.4., Table 3.). *H. major* and *S. pumilis* were both retrieved in the October '12 sampling though this difference in species presence/abundance did not result in a significant effect of treatment on overall phylogenetic diversity in this chapter.

The alien Symphypleona species, provisionally called '*Katianna* species 4' (Ardron 2009; Janssens 2014), KA '4', mentioned in Chapter 3., Section 3.4.4. and 3.5.2.1., see Figure 3.4.4.6. for images, was placed as a sister taxon to *Sminthurinus reticulatus* in Figure 4.4. and next to a clade containing *Sminthurinus aureus*, *Sminthurinus elegans* and *S. reticulatus*, in Figure 4.4.4.. The genus *Sminthurinus* is found within the Family Katiannidae, as is the genus *Katianna*, so this result supports the identification of the alien Symphypleona as a Katiannid species.

The analysis conducted here is sensitive to phylogenetic tree topology. Here there is reasonable support for most nodes and overall it fits the current taxonomic placement of species. A phylogenetic tree with greater support, possibly better fitting the data may have been achieved had the Bayesian analysis been run for longer or with more chains. The phylogenetic tree resolution within the Family Isotomidae may have been improved with more sampling or higher quality sequences, see Figure 4.4.. Given the nature of the analysis the former option would not have been appropriate, but the sequence used for *Folsomia spinosa* could have been more reliable. The *F. spinosa* sequence was not a consensus sequence as sequencing failed in one direction. There were no sequences available on GenBank that it could have been replaced with and the blast search revealed the most similar sequences to be from *Folsomia candida* and *Folsomia quadrioculata*

specimens, so the decision to still include this sequence was taken; the repercussions on PD and MPD calculations would have been greater had it been omitted. As the Isotomidae sequences used to construct the phylogenetic tree are all separate species that are relatively closely related, according to the taxonomy, this should not have been a problem for calculations of PD and MPD.

Across all the vegetation origin treatments it was not possible to identify ten out of 834 Collembola specimens to species level, so it was necessary for these to be excluded from the analysis. This may not have affected the PD calculations and comparisons; for eight of these excluded specimens the species it was most likely to be was already recorded as present within the plot, but it would have artificially lowered the MPD scores. The origin of the unidentified (and so excluded) specimens can be found in Table 3., Appendix 4.3.. Overall the majority were missing from the Native vegetation origin treatments (six specimens), it is unlikely to have affected the overall results.

4.5.2. Phylogenetic diversity: All sites

Ideally the Phylocom analysis would have been conducted across all sites to enable comparison between the RHS experimental 'flowerbed' plots, the adjacent grassland sites, Wisley Common and Buxton Wood. It would then have been possible to determine if the difference in taxonomic diversity was reflected in the phylogenetic diversity metrics; greater diversity in the non-garden habitats (Chapter 3., Figure 3.4.5.4. and Figure 3.4.5.5.).

Unfortunately this would not have been a valid comparison due to missing taxa and unequal sampling effort. With the vegetation origin treatments pooled, the RHS

experimental sites had three times the sampling effort of either Wisley Common or Buxton Wood, and six times the sampling effort of the adjacent grassland (due to unprocessed samples see Chapter 3. Section 3.2.2.), however, this analysis could be undertaken in the future.

Regarding missing taxa, there were two taxa unrepresented in the phylogeny; *B. arvalis* and *S. schoetti*, and it was necessary to download two sequences to construct the phylogeny: *E. marginata* and *S. ununguiculata*. Despite the concerns outlined in Section 4.1.3. these sequences fell where they were expected to; *E. marginata* was placed with other *Entomobrya* spp. and *S. ununguiculata* was placed with other Poduromorpha, although discretion was exercised during sequence selection, see Section 4.3.1.. Across all sites there was also a greater number of individual Collembola not identified to species level due to damage: 25 specimens.

From Figure 4.4.4., the dissimilarity in species community composition between the sites, found in Chapter 3. Figure 3.4.5.2., can still be seen for this reduced data set. Figure 4.4.4. suggests that there are moderate levels of diversity within the groups containing *Parisotoma notabilis*, *Protophorura armata* and *Mesaphorura macrochaeta*, however, they are all monophyletic and so they do not necessarily require greater consideration under the phylogenetic species concept (see Eldredge and Cracraft (1980); Nelson and Platnick (1981) and Wheeler (1999) for a discussion of its merits over the biological species concept). In Figure 4.4.4. the branch support values for the aforementioned sections are high, however, there is some room for improvement and this is still just a consensus tree composed from a generated set of 'best' trees. Phylogenetic trees are sensitive to all the species/sequences in them and, in a longer running analysis you are

more likely to obtain a better 'best' tree and more likely the correct one as sampling size increases.

Here the sampling would need to be much greater, requiring the identification of many other species taxonomically understood to belong to the same genera and sequences of species thought to be most closely related, and resulting in polyphyletic tree in order to warrant a revision of the current taxonomic understanding, see Agapow et al. (2004) for a discussion on the lumping and splitting of species which artificially inflates taxonomic species richness.

4.5.3. Relationship to taxonomic diversity and further work

Taxon richness has been shown to be decoupled from phylogenetic diversity for large datasets (Forest et al. 2007). Here the phylogenetic diversity was strongly correlated with species richness, which would be expected, especially for a small dataset. The total number of species retrieved from the RHS experimental plots during the October '12 sampling occasion was 25; Forest et al. (2007) used the entire flora of a biodiversity hotspot.

The soil biodiversity metrics calculated based on the phylogenetic information agree with those based on taxonomic methods; there is no overall significant difference in Collembola diversity between the different vegetation origin treatments corroborating the findings from Chapter 3..

In Chapter 3. differences in Collembola community composition were found across sampling occasions. Here is was not possible to compare the phylogenetic diversity

between the seasons or between the vegetation origin treatments for each season, as only the samples collected in October ’12 were used for the molecular work. In the future it could be possible to construct retrospective phylogenetic trees should reliable COI sequences for the missing data become available on GenBank, as the Collembola species data was recorded for each sampling occasion for Chapter 3..

Regarding the DNA extraction method used in this research DNeasy kits, there are now alternative non-destructive methods of DNA extraction which enable retention of voucher specimens so that morphological features can be re-examined in the light of the phylogenies their sequences produce (Hiroaki et al. 2015). These would have been preferable and if possible should be used in future similar studies.

A multi-gene approach is considered better when building phylogenies (e.g. Meyer, Witek and Lieb (2011)) unfortunately this was not within the scope of this research. A consensus tree could have been constructed from two or more concatenated gene regions, so that any conclusions drawn would have been more powerful. To achieve this it could have been possible to download and not necessarily do all the extraction, amplification or sequencing work (e.g. for a number of the Collembola species recorded in this study the 28S ribosomal RNA region was available on GenBank), however, again this would have placed a greater reliance on the sequence validity of other taxonomists and it undoubtedly would have created gaps in the trees where it was not possible to obtain both regions (see Section 4.1.3.).

In Phylocom it is possible to calculate Rao’s quadratic entropy (Rao 1982) an equivalent of the Simpson diversity index. However, this data subset was considered too small for a

meaningful analysis using those methods; a fraction of the species known to be present were retrieved during the October '12 sampling period. In Phylocom it is also possible to incorporate functional traits into phylogenetic trees (see Kraft, et al. (2007) and Webb et al. (2011) so the trait dispersal of a community can be compared and the structure of communities within phylogenies (Webb et al., 2002), however, these aspects was not relevant here, or explored due to analysis time constraints. In the future it could be interesting for comparisons between the Collembola species found in the different habitats.

The DNA sequence data obtained here could also have been used to address the following sub-questions had time permitted: to which of the *P. notabilis* lineages identified by Porco et al. (2012) do the *P. notabilis* specimens sampled at the RHS experimental plots belong and is this the same lineage across all sites (both RHS experimental plots, adjacent grassland sites, Wisley Common and Buxton Wood). Many Collembola species do exhibit pH preferences though *P. notabilis* is considered pH indifferent (Ponge 2000), as pH was found to be significantly different between sites in Chapter 2. (Section 2.4.1.), with both alkaline and acidic sites, it would have been interesting to see if the same *P. notabilis* lineage was present across all sites, and whether it was 'L0' (as this was the lineage identified at present based on one specimen in the analysis by Porco et al. (2012)). As all the sequences used in the Porco et al. (2012) analysis are available on GenBank it would have been interesting to rebuild the tree using a bayesian approach; it is also possible to constrain phylogenetic trees and it could have been determined if the tree presented by Porco et al. (2012) was significantly shorter than trees where the *P. notabilis* lineages were constrained together. Here, in Figure 4.4.4., the *P. notabilis* sequences all fell within a monophyletic group (including the

specimen it was not possible to build a consensus sequence for, see Table 1. Appendix 4.4.), although there were no congeneric taxa found that could have been able to split it according to Porco et al. (2012).

The sequences obtained here could still be used to provide insight into whether *S.reticulatus* is indeed a valid species or is actually a colour morph. To achieve this additional sequences may need to be down loaded from BOLD (only those associated with images unless the species definitions applied by the sequence author/collector are known) or extra molecular lab work undertaken.

This molecular work focussed on specimens retrieved during the October '12 sampling. For this occasion, across all sites, 49 species were retrieved and for the majority of these taxa successful sequences were obtained (45 species, equivalent to 92%), however, not all the species found over the full duration of the study were retrieved during this period. A total of 69 Collembola species (Table 3. Appendix 3.4.2.) were found over all six sampling occasions. There were differences in Collembola communities between seasons (Chapter 3., Figure 3.4.5.3.), so to obtain a complete picture, ideally this analysis would also have been undertaken for the other sampling occasions to ensure all species present were represented. However, as higher abundances were expected in the autumn (Petersen & Luxton 1982) and this season was more likely to reflect the average conditions of the site (Usher 1970) the October sampling occasion was the most logical choice for molecular work, especially when other factors were taken into consideration: Collembola taxonomic identification experience and scheduling with other data collection aspects of the research.

4.6. Conclusions

No significant differences in Collembola phylogenetic diversity were found between the plots planted with Native, Near native or Exotic vegetation. This research supports the conclusions from Chapter 3. which found no overall differences in Collembola taxonomic diversity between the vegetation origin treatments. The phylogenetic trees construction resulted in the sequencing of 25 specimens for species that there is currently no published data for the COI barcode region, 19 of these have no published data for any region. This data adds to the pool of available data for future Collembola phylogenetic work, of which there has been little published for Collembola communities globally and none for the UK. Here the conclusions from phylogenetic diversity align with those from the taxonomic assessment of species diversity.

From this research it has been established that the vegetation origin (Native, Near native, exotic) does not have a significant effect on diversity, either taxonomic or phylogenetic. Chapter 5. assesses whether or not vegetation origin has an impact on soil ecosystem function. It is discussed in relation to the Collembola biodiversity results as a whole as although no overall difference in biodiversity has been found (between the vegetation origin treatments) Chapter 3. found differences in soil fauna abundances.

Chapter 5. Ecosystem function

5.1. Introduction

5.1.1. Decomposition and ecosystem function

Decomposition is the process by which organic detritus such as plant litter breaks down and gets incorporated back into the soil profile; as well as being a key ecosystem service itself, it also supports the function of other 'services' provided by ecosystems, see Chapter 1., Section 1.6.. Previous studies have compared ecosystem function by looking at decomposition and nutrient mineralisation rates (Wieder & Lang 1982) although there are several other ecosystem processes that can be measured to provide an indication of function including community respiration, productivity and water or nutrient retention (Naeem et al., 1995). However, as decomposition is the aspect most studied within the literature, and is inextricably linked to the soil fauna, it was selected for comparison.

5.1.2. Main factors affecting decomposition

Soil organisms, climate and leaf litter quality have repeatedly been shown to independently influence decomposition rates (Smith & Bradford 2003; Aerts 1997; González & Seastedt 2001). A vast number and variety of soil fauna and microbes with complex interactions are responsible for the decomposition of organic matter (Seastedt & Crossley 1984), see Figure 5.1.2. for a soil food web diagram, with the roles played dependent on size (Cole et al., 2006; Coleman & Wall 2007).

Litter decomposition requires both micro-organisms and larger soil fauna (Swift et al. 1979b). The mesofauna have a regulatory effect on soil microbial communities influencing decomposition; reductions in microarthropod abundance can reduce rates of

decomposition (Heneghan & Bolger 1996). Microarthropod diversity has also been shown to be important; Ponge (1991) found that different Collembola species and species groups in the same microhabitat had different food preferences; they selectively graze on fungal hyphae mediating distribution and potentially reducing or enhancing decomposition rates (Newell 1984a; Newell 1984b). These studies demonstrate the importance of Collembola abundance and diversity (for which data were presented in Chapter 3.) and could be important for discussing any differences in decomposition rates between treatments and sites. It has also been suggested that Collembola could be of greater relative importance in the initial stages of decomposition as this period is associated with a rapid turnover of different fungal species (Frankland, 1966; Hopkin, 1997; Ponge, 1991).

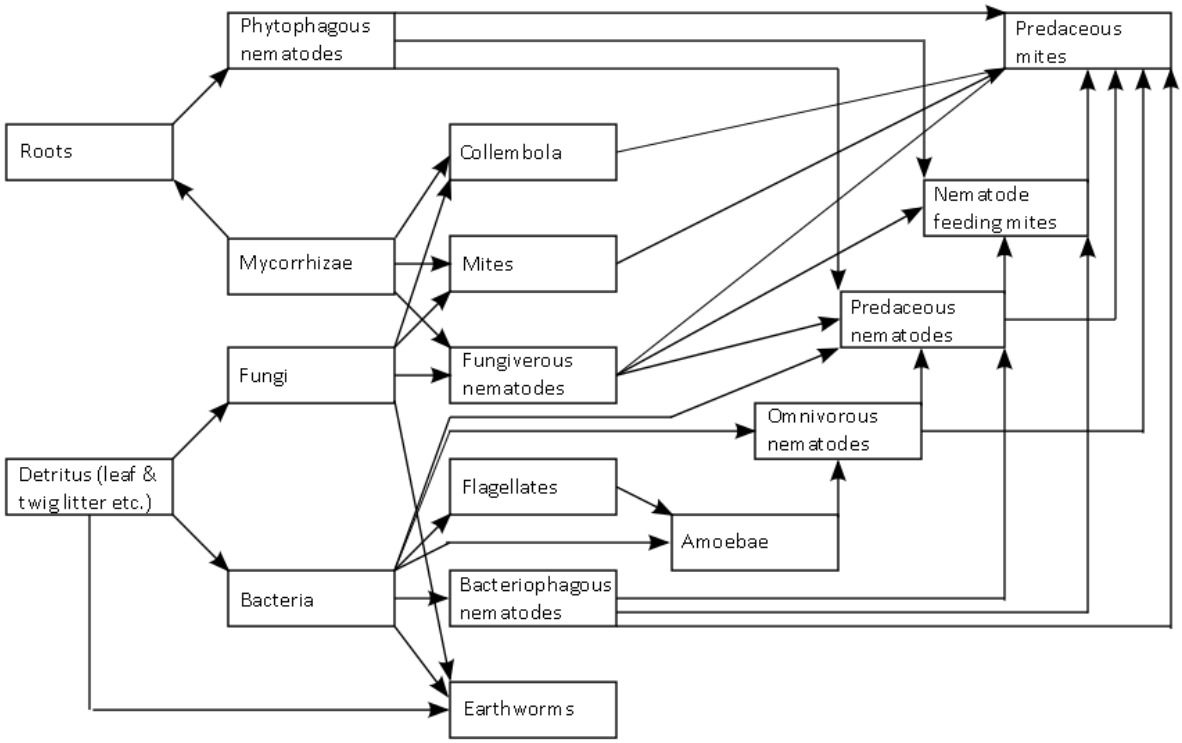

Figure 5.1.2. Soil food web diagram (adapted from Bardgett, 2002; de Ruiter, Neutel, & Moore, 1995).

Earthworms are soil ecosystem engineers (Jones et al. 1994) with a large impact on soil structure. Where they occur they play a fundamental role in decomposition and soil formation (Blouin et al. 2013). In decomposition processes they are particularly important in the initial break up and comminution of the litter. In European temperate grasslands,

through burrowing and casting activity, earthworms have been found to mix and displace between 6 Kg and 100 Kg metre^{-2} of soil each year (Lavelle & Spain 2005; Bouché 1975). The upper end of this estimate is unusually high; figures of around 2 Kg metre^{-2} year^{-1}, when looking at the fraction of soil transferred from deeper soil to the top soil, 6 Kg metre^{-2} year^{-1} for cast deposition (primarily epigeic species (Blouin et al. 2013)) and a total turnover of up to 20 Kg metre^{-2} year^{-1} are more reasonable and accepted (Bouché 1981; Müller-Lemans & van Dorp 1996). In the UK, Darwin (1881) estimated that this activity resulted in the accumulation of a layer of organic matter between 4.8 – 5.6 cm at the soil surface over a 10 year period (~ 5 mm per year) on English pastures favourable to earthworms.

Climate is one of the major factors affecting decomposition. Aerts (1997) reviewed the relationship between climate and litter decomposition, looking at data from 44 different locations under a range of climatic conditions. Across the sites a threefold increase in actual evapotranspiration was found from the temperate locations to the tropical sites which corresponded to a six fold increase in the decay constants. Studies have found an effect of both temperature (Gongalsky et al. 2008) and soil moisture content (Gabriel & Kellman 2014) on decomposition processes. The UK has a temperate climate with seasonal fluctuations, in addition to this affecting the abundance of particular groups of mesofauna it also impacts directly on decomposition. Repeated cycles of freezing and thawing, or drying and wetting, damage the integrity of plant cell walls and cause litter to become increasingly brittle and more easily fragmented (Jager 1967). All sites and treatments in this study are located close together, so they should have been subject to the same climatic conditions (see Chapter 2. Section 2.1.1.).

Plant litter quality affects the ability of soil fauna to facilitate decomposition (Wardle & Lavelle 1997). The final nitrogen concentration and the initial lignin content of litter have both been found to be highly negatively correlated with decomposition rates (Melillo et al. 1982). The lignin:N ratio of leaf litter has also been found to be a good predictor of decomposition rates, although not for temperate regions (Aerts 1997). Loranger et al. (2002) found that litter quality was the main determinant of litter decomposition; in addition to the importance of lignin content, decomposition rates were negatively correlated with initial phenol and tannin content and positively with the initial cellulose content. Smith and Bradford (2003) found that initial concentration of nitrogen was positively related to decomposition. These parameters vary between litter species and age of leaf, so it is very important for these factors to be controlled.

5.1.3. Monitoring decomposition

Three of the most widely used measures of decomposition are soil respiration, litter fall/standing crop quotients (K_L values) and litter bag dry mass loss (Aerts 1997). Leaf litter bags are a long-standing and commonly employed method of assessing decomposition (Bocock & Gilbert, 1957; Grant, 2002; Huhta, 2007; Wieder & Lang, 1982) and so are used here.

Decomposition rates are not found to be linear, with periods of rapid mass loss, followed by near-stasis, see Howard and Howard (1974). Decay constants can be easily calculated assuming a first order decay model: $k_t = \ln W_t - \ln W_0$ (W_t = final mass, W_0 = initial mass) (Swift et al. (1979) and references therein, but see Manzoni et al. (2012) for a comparison of decomposition models for analysing litter bag data). Twig litter bags have previously been used in conjunction with leaf litter bags (e.g. Naeem et al., 1995) as they provide a

second timescale for the comparison of decomposition rates, due to the increased lignin content and correspondingly slower decomposition rates, with the additional benefit of being easier to handle.

An important consideration in litter bag design is the size of the holes in the mesh used to make them; litter bags varyingly under or overestimate decomposition rates depending on the size of the holes in the mesh used. Over estimation due to the activity of macrofauna ingesting the litter inside and then defecating the unassimilated portion outside of the litter bag and also due to the larger holes required for their access meaning that litter fragments commute out more easily (Smith & Bradford 2003), although, this can permit soil particles to enter more freely. Conversely, if the holes are less than 2 mm, although the litter is accessible to all components of the micro and mesofauna the macrofauna are excluded and so their activity is unrecorded. However, they are still a useful tool in enabling comparisons of treatments (Coleman et al., 2004). Litter bags have been used to study earthworms (Butt & Lowe 2004) with holes of 3 mm being used, however, this means their activity cannot be teased apart from that of other soil organisms.

To get a full picture of ecosystem function it is important to include earthworm activity. As the mesh used inside the Berlese-Tullgen funnels during soil fauna extraction was too fine for macrofauna to pass through, earthworm abundances were not recorded for analysis in Chapter 3.. In order to incorporate this important soil fauna group into this study and more fully cover decomposition processes it was necessary to employ additional techniques.

Methods to investigate earthworm abundance and community structure do exist; such as formaldehyde/formalin (Raw 1959) and allyl isothiocyanite (AITC) (Zaborski 2003), however, aside from posing a health risk these have negative impacts on plant and soil communities; where they have been tested in the literature they have been applied to areas larger than would be possible within the plots (0.707 m^2: Valckx et al. (2011) and 0.25 m^2: Iannone et al. (2012)). These methods are unsuitable for experiments where destructive sampling would have negative impacts on the overall design and monitoring of other aspects of biodiversity, such as the 'Plants for Bugs' project. A less hazardous and damaging method for sampling earthworms is ground hot mustard. Chan and Munro (2001) found it to be more efficient than formalin although efficacy was dependent on the functional group investigated (endogeic vs anecic), whilst Iannone et al. (2012) found it to be as effective as AITC. Reviewing current methods Valckx et al. (2011) highlighted the additional preparatory work that would be required for concentration optimisation and after consideration, for this study, it was decided that it was too destructive given the size of the plots. Electroshock devices are a less invasive method, they are used to generate electric fields and are applied over smaller areas resulting in little or no disturbance and no contamination (Weyers et al., 2008). However, in 2009, the equipment still cost $3000 (Butt & Grigoropoulou 2010) and this method, more importantly, is unable to provide a measure of ecological function.

Developed by Von Törne (1990) as a method for monitoring soil fauna activity, bait lamina strips have been found to effectively capture soil macrofauna activity (André, et al., 2009). Gestel et al. (2003) conducted a set of mesocosm experiments testing a range of methods for assessing the biological activity of soil fauna including the application of bait lamina strips. They found that bait consumption in the mesocosms containing only the

Collembola or Acari were not significantly different to that of the controls, concluding that the bait lamina strips provided the best indicator of earthworm activity as the bait consumption increased with increasing earthworm densities. These findings were echoed by Gongalsky et al. (2008) who also determined that they did not register microbial decomposition. Although other previous studies did find Collembola and Enchytraeid abundance to be correlated with bait lamina consumption (i.e. Heisler & Brunotte (1998) and Helling, Pfeiff, & Larink (1998)), Gestel et al. (2003) pointed out that in the first case earthworm densities also increased, whilst an unrealistically high Collembola density was used in the second study (100 Collembola in 75 g): it was 13 times greater than that used by Gestel et al. and 27 times higher than the median density of Collembola found in this study (Chapter 3., Section 3.4.). In fact densities were twice as high as the highest density of Collembola found in this study (1333 Collembola per kg and 621 Collembola per kg, respectively).

This study used the two native species *Betula pendula* Roth (silver birch) and *Quercus robur* L. (English oak) for the leaf and twig litter bags, respectively. Leaves of these plant species have previously been tested in decomposition studies (Cornelissen 1996) whilst silver birch twigs have been used by Naeem et al. (1995). These tree species were selected due to their widespread use within the literature and because their statuses as native to the UK are well supported (Birks 1980). Both these tree species were growing on land owned by the RHS and there were sufficient quantities of material available so that *Q. robur* leaves and *B. pendula* twigs could all be harvested at the same time and decomposition state (see Section 5.2.2. and 5.2.3.), but they were not being grown within the plots themselves and so issues of a decomposition 'home-field advantage' (e.g. Ciska Veen et al., (2014)) were avoided.

Although a Native/ Near native/ Exotic crossover of litter material for litter bags (i.e. each plot containing litter from each of the treatments) could have been very interesting, unfortunately it was not considered possible within the scope of this piece of research. This was for several reasons, the foremost being the size constraints of the plots (3 m by 3 m) and the disturbance deploying two additional litter bag sets within each of the plots would have caused, especially considering the other experimental work and sampling already taking place. There would also likely have been difficulties encountered with sourcing adequate quantities and ensuring the homogeneity of plant material between the bags. Enough material of a similar quality/decomposition state would have had to have been collected, from each of the treatments, to fill at least 36 bags.

Therefore, in order to determine the impact of Native, Near native and Exotic planting on ecosystem function, native leaf/twig litter bags and bait lamina strip were used. The combination of both litter bags and bait lamina strips allows interpretation of the decomposition activity of specific groups of soil fauna organisms. Two of the major factors: climate and litter/bait quality are controlled across the treatments. For the remaining factor; soil organisms, the abundances and diversity of components of the mesofauna were determined and are available in Chapter 3. In Chapter 3. no difference was found in terms of the species diversity indices measured or the community composition between the vegetation origin treatments, although there were differences in abundance and differences in the other parameters were generally greater when comparing the different RHS experimental sites. Other studies have looked at decomposition between different planting treatments and habitats, finding evidence of a 'home-field advantage' (e.g. Ciska Veen et al., (2014)), whereby litter decomposes fastest underneath plants of the same material. From this it could be expected that the birch and

oak litter decomposition would be the same across all the vegetation origin treatments as neither of these species are grown in any of the treatments. In terms of the soil parameters measured in Chapter 2., aside from the explainable difference in Mg, there were no significant differences in the soil properties between the vegetation origin treatments. This meant that any observed differences were likely to be due to differences in soil microflora/microfauna, the differences noted in mesofauna abundance or changes in microclimate due to vegetation structural differences (cover or density) between plots. Differences in soil fauna communities; their taxonomic diversity and abundance, and soil properties, were greater across all the sites than within either Deer's Farm, or Howard's Field. So it was expected that differences in decomposition were more likely to be found across all sites than within the vegetation origin treatments.

As there was no difference in diversity for the component of siol biodiversity assessed (Collembola) in either Chapter 3. or 4. the decomposition analyses were conducted with the null hypothesis (H0): all the percentage dry mass lost values/decomposition rates belong to the same population and the alternative hypothesis (Ha): at least one of the vegetation origin treatments does not belong to the same population.

5.2. Methods

5.2.1. General methods

The study site descriptions and plot treatments are as described in Chapter 2., Section 2.1. Where plot pH has been included in the decomposition analysis models, this data was the mean pH taken across all the soil cores from each plot from the Roehampton soil analysis (as these were the pH values used in Chapter 3.). The pH value for each RHS experimental plot came from the mean of all soil cores collected for each sampling

occasion: July ‘11, October ‘11, April ‘12, July ‘12, October ‘12 and April ’13, since the adjacent grassland, Wisley Common and Buxton Wood sites were not sampled in July ‘11 their plot pH values are a mean of the other ten soil cores.

5.2.2. *Quercus robur* leaf litter bags

To investigate differences in micro/mesofauna decomposition activity between the treatments, and sites, *Q. robur* leaf litter bags were used. Freshly senesced *Q. robur* leaves were collected on the 24/9/12, entire leaves were selected without galls or visible leaf miner activity. These were dried at 105 ˚C for five days. The leaf litter was divided between the litter bags, weighed, with the total initial dry mass recorded (mean total initial leaf dry mass per plot: 4.03 g, s.d. < 0.01 g).

120 bags were made from plastic mesh with holes of a 2 mm gauge (purchased from Squires Garden Centres). This was cut to 20 cm x 40 cm rectangles, folded in half and sealed (Tew Direct Heat Sealer, THS 200) along the edges adjacent to the fold to create a pocket into which the dried leaves and a plastic plant label with the plot code were placed inside before the top edge was also sealed. As the plastic was prone to melting and sticking to the heating element of the heat sealer, greaseproof paper was used as a barrier to prevent this and peeled off afterwards.

Two litter bags per plot were buried on the 28/9/12 at a random position (see Appendix 5.2., Figures 1.-6.) within each of the plots, following the random sampling methods detailed in Chapter 3., Section 3.2.1., with a cane marker to aid in later location. The litter bags were then retrieved after 6.5 months (11/4/13) and re-dried at 105 ˚C for five days (as in Bocock and Gilbert (1957)). Bocock and Gilbert (1957) left the litter bags out for

only six months, but as this was because decomposition rates were being compared with leaves that decomposed faster (i.e. *Betula verrucosa*), the additional two weeks would only have served to accentuate any differences. The *Q. robur* leaves had the smallest percentage dry mass loss of the leaves that were looked at by Bocock and Gilbert (1957) so they could afford to be left in for longer. The leaves were carefully handled and residual soil delicately removed with a fine paintbrush so that the leaves could be reweighed, the final dry mass recorded and the percentage difference in mass lost calculated.

5.2.3. *Betula pendula* twig litter bags

To investigate differences in micro/mesofauna decomposition activity between the treatments, over a longer timescale, *B. pendula* twig litter bags were used. A plastic mesh with holes of a 2 mm gauge was used to make the litter bags (27.5 cm by 12 cm), each consisting of four heat sealed compartments filled with *B. pendula* twigs of a known dry mass, see Figure 5.2.3..

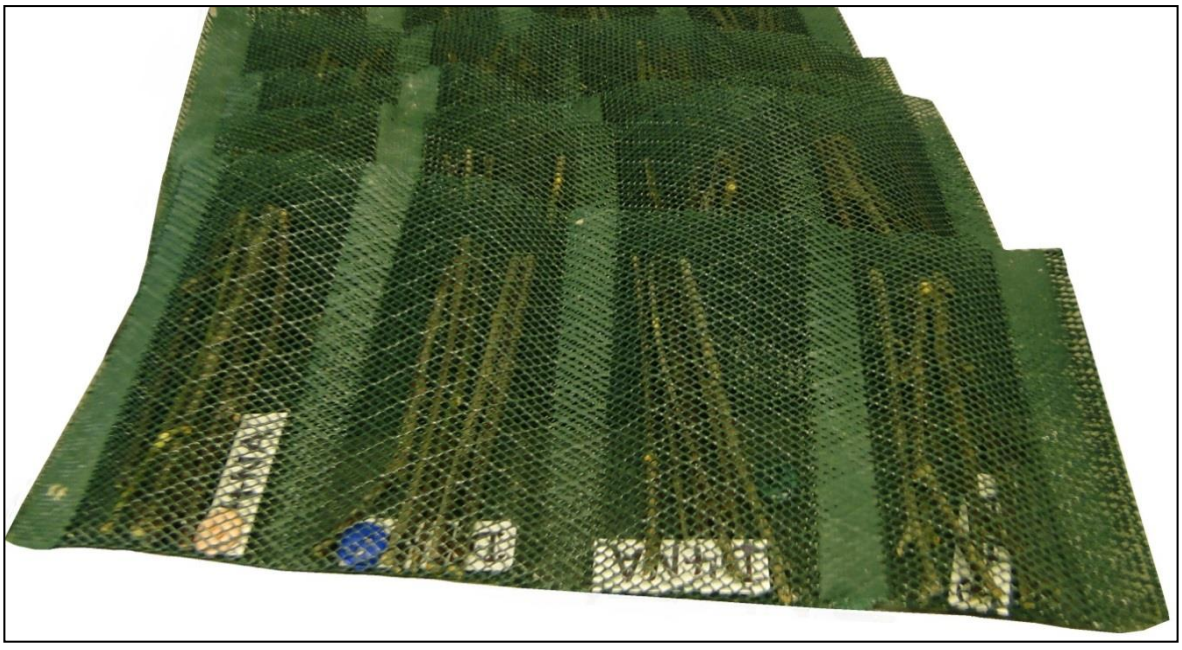

Figure 5.2.3. Prepared *B. pendula* twig litter bags, prior to sealing of top edge. Photograph adapted from one provided courtesy of the RHS (Bostock, 2011).

Betula pendula branches were harvested from a single tree (12/12/11) and cut to lengths of 10 cm (a standard size e.g. Pandey, Sharma, and Bargali, 2006). These twigs were dried at 105 ˚C for five days and separated into three size categories based on the measurement of diameter at the centre point: small (1.5-2.49 mm), medium (2.5-3.49 mm) and large (3.5-4.49 mm). Bundles of six twigs were prepared for each compartment, each comprising three small, two medium and one large twig, to ensure that the surface area as well as mass was kept as constant as possible between bags. Each bundle was weighed and the total initial dry mass recorded (bundle mean initial dry mass range: 3.76 g to 3.85 g). A small coloured plastic token was also sealed within each compartment; a dark coloured token in the first compartment and light coloured tokens in the remaining compartments to facilitate removal of the required bag in the field, and a plastic plant label with the plot code to enable identification of litter bag plot origin in the lab.

The litter bags were buried on the same day (21/12/11; incidentally the same date as Bocock and Gilbert (1957) set theirs out, just 56 years later) at a random position within each of the plots, following methods detailed in Chapter 3., Section 3.2.1., at a controlled depth of 1.5 cm (as in Naeem et al. (1995) who also used *B. pendula* twigs, as two of the factors influencing decomposition; temperature and soil moisture, vary with depth (Hunt 1977)). Cane markers were added to aid in later location of the bags (a combination of iron nails, as a marker, and a metal detector proved ineffectual (possibly the result of magpie interference)). After 6, 12, 18 and 24 months a compartment was cut off each litter bag (harvesting dates: 20/6/12, 13/12/12, 20/6/13, 26/12/13). Each compartment was re-dried at 105 ˚C for five days and cut open with the twigs carefully removed. Residual soil was dusted off with a fine paintbrush before the twigs were reweighed and final dry mass recorded.

5.2.4. Bait lamina strips

A field technician, Michael Terrington, was supervised in making and deploying the bait lamina strips, monitoring bait consumption and recording associated co-variate data. A sheet of PVC 1.5 mm thick was cut into strips of dimensions 25 cm by 1 cm using a jigsaw. 15 holes 2.5 mm in diameter were then drilled through at 1 cm intervals starting at a position 0.5 cm from the soil surface when the strips were inserted into the ground, see Figure 7., Appendix 5.2.. One end of each strip was sprayed with yellow aerosol paint to facilitate strip location, whilst the other was cut to a point so that it could be inserted more easily into the ground.

The holes were filled with a standard mixture of cellulose, bran flakes and activated charcoal in the ratio 70:27:3 as used by Kratz (1998), Gestel et al. (2003) and Simpson et al. (2012), the latter study showed this bait to be the best indicator of trophic activity compared to three others where the bran flakes were replaced with either *Fraxinus excelsior* L. (ash), *Acer pseudoplatanus* L. (sycamore) or *Q. robur*. Distilled water was added to turn it into a paste then the holes were manually filled and allowed to dry, as when the bait dries it contracts holes were refilled and allowed to dry again (Simpson et al. 2012).

Four strips per plot were deployed on the 20/06/13 at a random position (following methods detailed in Chapter 3., section 3.2.1.) within each of the plots. A rasp, of the same dimensions as the bait lamina strips, was used to make a vertical hole into which the strips were inserted. Bait consumption (the number of holes perforated) was recorded after 5, 8, 11, 14, 20, 32 and 54 days, in situ with the strips returned to the plots, as in Gestel et al. (2003).

Although Gongalsky et al. (2008) did not find a significant effect of soil moisture on bait consumption, co-variate data was still recorded per plot; soil moisture content readings (taken as percentage volumetric water content) were made using a Delta HH2 moisture meter and a Delta SM200 soil moisture sensor, as in Chapter 3., Section 3.2.3., on the 20/06/13 and then each day the bait lamina strips were checked for bait consumption. This meter measures the soil moisture content across the top 5 cm of the soil profile, so although it did not extend the full depth of the bait lamina strips, it enabled soil moisture comparisons between plots. A mean soil moisture value was calculated for each plot for the period of bait lamina strip exposure.

Previously soil temperature was also recorded as a potential co-variate in bait lamina activity studies (e.g. Simpson et al., (2012) although it was later excluded from analysis). It was decided not to include soil temperature in this study as time was a limiting factor and it was more important to have all the strips assessed for activity on the same day. Although each of the plots could have had slightly differing microclimates due to the structure of the plants growing above them, geographically they were all within a circle with a radius of 560 m centred on TQ 06837 59144 (see Chapter 2., Section 2.1.1.) so differences were not considered likely to be great.

5.3. Analysis

All statistical analysis was conducted in RStudio (RStudio, 2014), versions “Roasted Marshmallows”, “Warm Puppy” and “Spring Dance”. Prior to analysis, histograms were plotted to get a feel for the data distributions. When analysing decomposition data, which is generally percentage dry mass remaining/lost, arcsine square root transformations (angular transformations) used to be routinely applied, with this still being common place

within the literature as recently as 2012 (see Milcu and Manning, (2011) and Simpson et al. (2012)). The arcsine transformation is used to overcome the problem of the data being bounded between 0 and 100 as it stretches out both tails of a distribution and compresses the middle: it is used to normalise data (Sokal & Rohlf 1995). Arcsine transformations are recommended in several statistics books for life scientists: for percentage and proportion data (e.g. McKillup, 2005). For original data falling between 30% and 70% it is not considered essential to transform the data (Sokal & Rohlf 1995), however, if the majority of percentage changes are less than 20% or greater than 80% (for the *Q. robur* litter data 12% of the percentage dry mass lost values fell beneath this lower bound), it is considered particularly necessary (Crawley 2005). However, analysis approaches are changing; as a tool for ecologists arcsine transformations are being superseded by more modern methods. It is now being argued that these transformations should no-longer be used: improved methods have been developed with more appropriate logistic regression/generalised linear models (GLM)/generalised linear mixed models (GLMM) where the data distribution can be built into the models (Warton & Hui 2011; Wilson et al. 2013). Another method suggested to analyse decomposition data is to add the initial dry mass in as a co-variate and set the final dry mass as the dependent variable (Crawley 2005), so that the dependant variable is not converted to a percentage. To avoid model redundancy, here normally distributed data (Shapiro-Wilk: $p > 0.05$) were analysed using ANOVA and general linear models (glm), while data not fitting the normal distribution were analysed by Kruskal-Wallis and using generalised linear models (GLM). For both modelling methods a global model was built with different link functions explored, a starting model was selected based on the Akaike information criterion (AIC values) which provide a measure of the efficiency of the model and the adjusted R^2 value; the proportion of variance in the dependent variable that has been explained by the

model. Backwards step-wise deletion of non-significant terms and interactions followed using the 'drop1 function'. The resulting models were validated; the assumptions of normal distribution of residuals (Q-Q plot), homogeneity of variance and independence of variables (checked using Pearson correlation coefficients between pairs and using the Durbon-Watson test for serial autocorrelation). It was also checked, at each stage, that no points were excessively influential (Cook's distance).

5.3.1. *Quercus robur* leaf litter bag analysis

For the RHS experimental plot data the percentage dry mass lost from the *Q. robur* leaf litter bags was not normally distributed (Shapiro-Wilk: $p = 0.0039$), even after an arcsine transformation (Shapiro-Wilk: $p = 0.0038$), so the untransformed data was used. As the sample size was small a two-way ANOVA was still considered the most appropriate, but the alternative non-parametric Kruskal-Wallis test was also performed and is reported in the appendices, with the null hypothesis (H0): all percentage dry mass losses belong to the same population and the alternative hypothesis (Ha): at least one of the treatment or sites does not belong to the same population. However, only generalised linear models using the original untransformed data were built.

For the RHS experimental plot models percentage dry mass lost was the dependent variable, with 'site' (Deer's Farm or Howard's Field), 'treatment' (vegetation origin: Native, Near native or Exotic) and 'planting mix' (A, B, or C; nested within 'treatment' as planting mix A of the Native treatments is not equivalent to planting mix A of the Exotic treatments etc. included as independent variables, with 'pH' included as a co-variate (one pH value per plot). All first order interactions were included in the starting models. A Quasi-Poisson starting model (link = log) was selected based on adjusted R^2 values (AIC

values are unavailable for this family of distributions in R) and the plots of the residuals. The null hypothesis (H0): all the figures for percentage dry mass lost between the vegetation origin treatments belong to the same population ('treatment' not a significant factor), was used, with the alternative hypothesis (Ha): at least one of the treatments does not belong to the same population ('treatment' a significant factor in the final models).

For the comparison between the RHS experimental plots and their adjacent grassland a generalised linear model was built with the untransformed percentage dry mass lost data as the dependent variable with the main effects of 'site' (Deer's Farm, Howard's Field) and 'habitat' (RHS experimental plot, grassland), with 'pH' as a co-variate, and all first order interaction terms. A starting generalised linear model based on an Inverse Gaussian distribution was selected (link = inverse) based on AIC values, adjusted R^2 values and the plots of the residuals. Backwards step-wise deletion of non-significant terms and interactions followed. As the design was not balanced and as an interaction effect was found to be significant a Type III ANOVA was performed to give significance levels for the remaining factors in the final model.

When the leaf litter bag data from all sites (RHS experimental plots, adjacent grassland, Wisley Common and Buxton Wood) were considered, they were found to be normally distributed (Shapiro-Wilk: $p > 0.05$), although this was improved by an arcsine transformation (Shapiro-Wilk: $p > 0.1$). A one way ANOVA was performed with 'site' (Deer's Farm, Deer's Farm adjacent, Howard's Field, Howard's Field adjacent, Wisley Common and Buxton Wood) as the independent variable. The post-hoc Tukey's HSD test was performed where for an ANOVA factor $p < 0.05$.

A generalised linear model (Inverse Gaussian distribution) was built with the untransformed percentage dry mass lost data as the dependent variable with the main effects of 'site' (Deer's Farm, Deer's Farm adjacent grassland, Howard's Field, Howard's Field adjacent grassland, Wisley Common, Buxton Wood), with 'pH' as a co-variate, and the interaction term between 'pH' and 'site/habitat'. General linear models with the functions; log, inverse and identity were explored, the link function inverse gave the lowest AIC value (468.44), but the generalised linear models based on an Inverse Gaussian distribution all gave lower AIC values with the Q-Q plots indicating a better fit. The link function log was selected based on AIC values, adjusted R^2 values and the plots of the residuals.

5.3.2. *Betula pendula* twig litter bag analysis

Decay constants were calculated based on the difference in mass lost between burial and retrieval dates (0-6 months, 0-12 months, 0-18 months, 0-24 months), using a first order decay model: $k_t \ln = \ln W_t - \ln W_0$, see Section 5.1.3. Neither the twig litter bag percentage dry mass lost data nor the decay constants were normally distributed for either the entire data set or just the RHS experimental plots (Shapiro-Wilk: $p < 0.05$), arcsine transformations did not rectify this. As for the leaf litter bags, generalised linear models were built in R using percentage dry mass lost as the dependent variable. The main effects were 'site' (Deer's Farm or Howard's Field), 'treatment' (vegetation origin: Native, Near native or Exotic), 'planting mix' (A, B or C; nested within 'treatment'), 'months buried' (6, 12, 18 and 24), and with 'pH' included as a co-variate. The first order interactions including 'planting mix' were not included in the starting model, due to unretrieved litter bags limiting sample size (i.e. D5ZB, H5EB). A starting model based on

the Inverse Gaussian (link = inverse) was selected according to AIC and adjusted R^2 values and the plots of the residuals, although gamma distributions also fit well.

In R Studio second degree polynomials were fitted to the data for each treatment and site separately. Decay rates were required per plot and as some litter bags were lost it was not possible to fit polynomials to the plot dataset due to a lack of degrees of freedom; there were only four litter bags per set and in the instances all bags were retrieved there was only one degree of freedom for the error. To obtain decay rates for the majority of the plots, the percentage dry mass remaining data was log transformed and then linear regression models fitted (this was possible for 34 of the 36 RHS experimental plots, as two litter bag sets were completely unretrieved). The gradients were determined (normally distributed: Shapiro-Wilk: $p > 0.05$) and analysed via general linear models so that any differences in decay rates between the RHS experimental plot treatments and across all sites could be assessed.

For the RHS experimental plot decomposition rate data models (Gaussian distribution, link = identity) were built with the main effects: 'Site' (Deer's Farm or Howard's Field), 'treatment' (vegetation origin: Native, Near native or Exotic), 'planting mix' (A, B or C; nested within 'treatment') and with 'pH' included as a co-variate. As for the percentage dry mass lost analysis, all first order interaction terms aside from 'planting mix' were included. The null hypothesis (H0): all the decomposition rates of the vegetation origin treatments belong to the same population ('treatment' not a significant factor), was used, with the alternative hypothesis (Ha): at least one of the treatments does not belong to the same population ('treatment' a significant factor in the final models).

For the comparison between the RHS experimental plot decomposition rates and those of their adjacent grassland, models (Gaussian distribution, link = identity) were built with the main effects of 'site' (Deer's Farm, Howard's Field) and 'habitat' (RHS experimental plot, grassland), with 'pH' as a co-variate, and all first order interaction terms. For the decomposition rate data from all sites models were built (Gaussian distribution, link = identity) with the main effect of 'site' (Deer's Farm, Deer's Farm Adjacent grassland, Howard's Field, Howard's Field Adjacent grassland, Wisley Common, Buxton Wood), 'pH' as a co-variate, and the interaction term between 'pH' and 'site'. Pearson's correlation coefficients were calculated using the mean pH and the soil property parameters measured in the NRM analysis (Chapter 2., Section 2.4.).

5.3.3. Bait lamina strip analysis

As in Simpson et al. (2012), feeding activity was analysed as the percentage of holes perforated, meaning that data was discrete and bounded between 0 and 100. Simpson et al. (2012) arcsine transformed their data prior to analysis before analysing using generalised linear additive models, however, it was not mentioned how they dealt with the bait lamina strips that recorded no activity; feeding activity in their study ranged between 0 and 75%. Here, as for the *Q. robur* twig litter bag data, the percentage of intact bait holes per plot (all four strips added together) was log transformed and then linear regression models fitted. This was possible for all plots. The gradients were not normally distributed (Shapiro-Wilk: $p = 0.04$, $p = 0.02$ and $p = 0.00054$ for the RHS experimental plots, RHS experimental plots + adjacent grassland and all sites, respectively), however, it was found that for all of the datasets starting models based on the Gaussian distribution (link = identity) fit best.

For the RHS experimental plots, rate of bait consumption was the dependent variable with 'site' (Deer's Farm or Howard's Field) and 'treatment' (vegetation origin: Native, Near native or Exotic) as the independent variables. 'Soil moisture' and 'pH' were included as co-variates. All first order interactions were included in the starting model, however, 'planting mix' was excluded. Preliminary models including it were unstable during stepwise deletion of non-significant terms and as there was only two plots with each planting mix under each treatment at each site had it ended up as a significant factor there would have been concerns as to the reliability of conclusions drawn based on those results due to the small sample size. As the design was not balanced and as an interaction effect was found to be significant a Type III ANOVA was performed to give significance levels for the remaining factors in the final model. The null hypothesis (H0): all the figures for bait consumption between the vegetation origin treatments belong to the same population ('treatment' not a significant factor), was used, with the alternative hypothesis (Ha): at least one of the treatments does not belong to the same population ('treatment' a significant factor in the final models).

For the comparison between the rates of bait consumption between the RHS experimental plots and their adjacent grassland models were built with 'site' (Deer's Farm or Howard's Field) and 'habitat' (RHS experimental plot or grassland) included as independent variables, with 'pH' and 'soil moisture' as co-variates, and all first order interaction terms. When the bait consumption was considered across all sites 'site' (Deer's Farm, Deer's Farm adjacent grassland, Howard's Field, Howard's Field adjacent grassland, Wisley Common, Buxton Wood) was the independent variable, with 'pH' and 'soil moisture' as co-variates, and first order interactions. Again a Type III ANOVA was

performed to give significance levels for the remaining factors in the final model as there were significant interaction effects and the design was unbalanced.

As the bait lamina strips had holes drilled at 1 cm intervals and four strips were inserted into the soil per plot, at each depth in each plot there were four holes. This meant that the bait consumption at each depth could also be explored. Pearson's correlation coefficients were calculated for the percentage of intact bait holes at each site at all 15 depths after 54 days (the length of the study).

5.4. Results

5.4.1. *Quercus robur* leaf litter bags

All leaf litter bags were retrieved, see Table 1., Appendix 5.4.1., for the initial and final dry masses.

5.4.1.1. RHS experimental plots

A two-way ANOVA showed no significant difference in percentage dry mass lost between either the vegetation origin treatments, the two RHS experimental sites, or their interaction, see Table 2., Appendix 5.4.1. and Figure 1. Appendix 5.4.1. for the full ANOVA results including interaction terms and the plots of the residuals, respectively. The corresponding H0 was accepted, see Figure 5.4.1.1. for the percentage dry mass lost under each treatment for the RHS experimental sites.

A GLM based on the percentage of dry mass lost from the *Q. robur* leaf litter bags also found that neither vegetation origin treatment, nor planting mix, nor RHS experimental site, nor pH, significantly affected the percentage dry mass lost. H0 was accepted. All

interaction terms were removed during the stepwise deletion of non-significant terms, until 'site' and 'treatment' remained in the final model, neither of which was significant. See Figure 2., Appendix 5.4.1., for the plots of the residuals from the initial global model and Figure 3., for the plots of the residuals from the final model where only 'site' and 'treatment' remained.

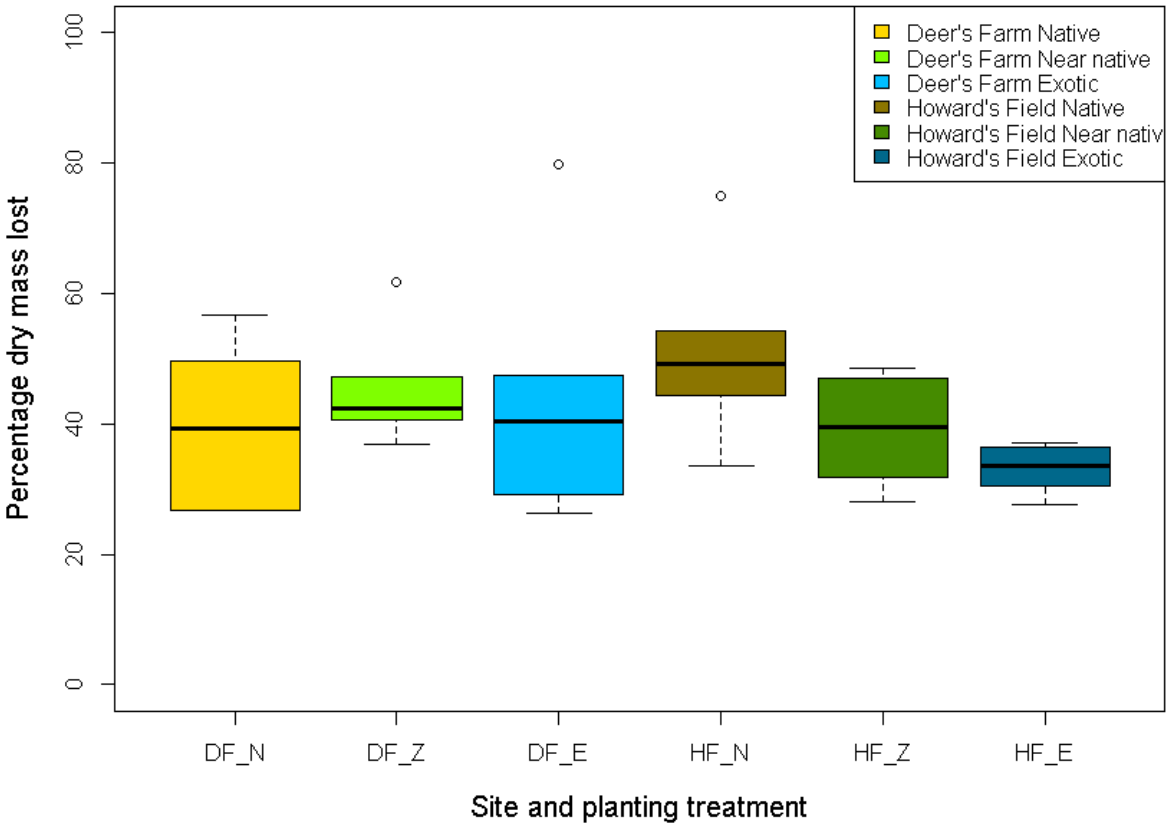

Figure 5.4.1.1. Boxplots of percentage dry mass lost of *Q. robur* leaf litter bags after 6.5 months under each of the RHS experimental plot treatments (N: Native (yellow), Z: Near native (green), E: Exotic (blue), at the two sites Deer's Farm and Howard's Field).

5.4.1.2. RHS experimental plots and adjacent grassland

A GLM based on the non-transformed percentages of dry mass lost from the *Q. robur* leaf litter bags found that percentage dry mass lost was significantly associated with 'habitat'; the RHS experimental plot litter bags had lower final dry masses than those of the adjacent grassland, see Table 5.4.1.2.. The interaction between 'site' (Deer's Farm or Howard's Field) and 'habitat' was significant, but neither 'site', nor 'pH' were found to

significantly affect percentage dry mass lost. All interaction terms including pH were removed during stepwise deletion of non-significant terms. See Figure 4., Appendix 5.4.1., for the plots of the residuals from the initial global model and Figure 5., for the plots of the residuals from the final model.

Table 5.4.1.2. Type III analysis of variance table for the significant terms in RHS experimental plot and adjacent grassland Q. robur leaf litter bag decomposition model: Adjusted R^2 = 1, AIC = 334.15, error: 44 d.f..

Term		d.f.	F value	p value	
Habitat	(RHS plot or grassland)	1	240.23	p = 2.2 e-16	***
Site	(DF or HF)	1	0.21	p = 0.65	NS
Site: Habitat	(interaction)	1	117.22	p = 5.4 e-14	***

NS: p > 0.05, *: p < 0.05, **: p < 0.01, ***: p < 0.001

5.4.1.3. All sites

A one-way ANOVA test revealed a significant difference in percentage dry mass lost between the leaf litter bags buried at the different sites: Deer's Farm, Deer's Farm adjacent, Howard's Field, Howard's Field adjacent, Wisley Common and Buxton Wood ($F_{5, 54}$ = 15, p < 0.001), see Figure 5.4.1.3. for a graphical representation. See Appendix 5.4.1., Table 3. and Figure 6. for the Tukey HSD tests and the plots of the residuals, respectively.

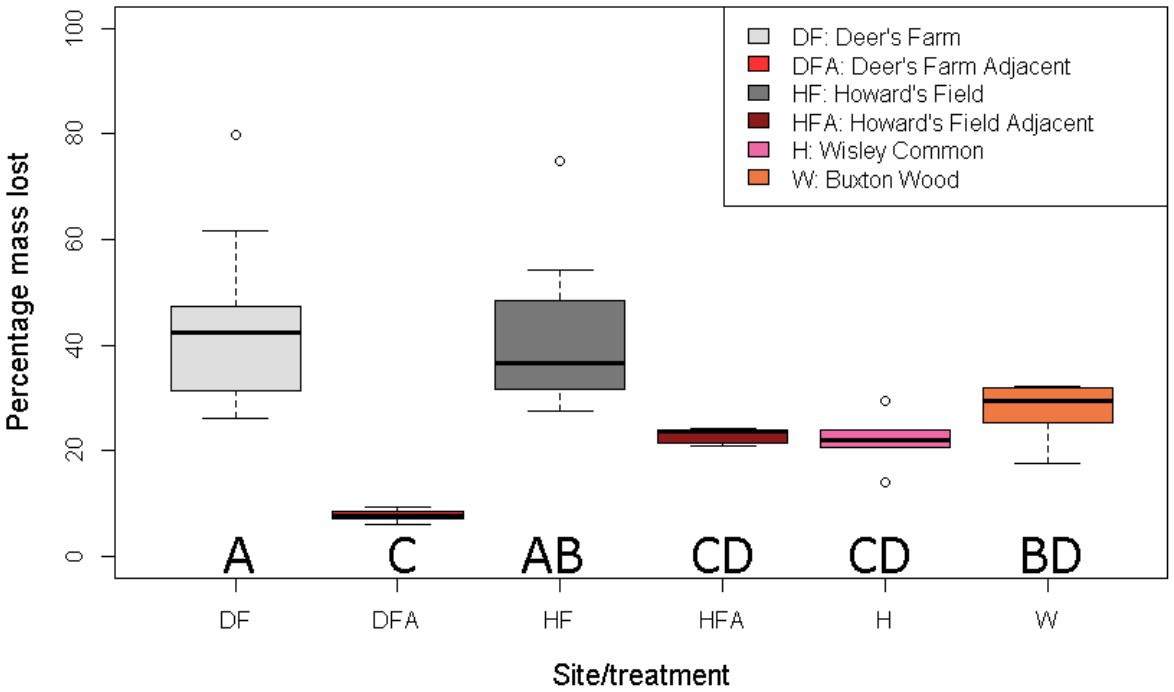

Figure 5.4.1.3. Boxplots of percentage dry mass lost of *Q. robur* leaf litter bags after 6.5 months at each of the sites (DF: Deer's Farm RHS experimental plots, DFA: Deer's Farm Adjacent plots, HF: Howard's Field RHS experimental plots, HFA: Howard's Field Adjacent plots, H: Wisley Common, W: Buxton Wood). Sites underneath the same letter do not differ ($p > 0.05$) according to the Tukey HSD post-hoc test.

A GLM performed on the non-transformed *Q. robur* leaf litter bag data found significant differences in percentage dry mass loss between the different sites: Deer's Farm, Deer's Farm adjacent grassland, Howard's Field, Howard's Field adjacent grassland, Wisley Common and Buxton Wood ($F_{5, 54} = 57.789$, $p < 0.001$). pH was not found to significantly affect percentage dry mass lost and was removed during stepwise deletion. See Figure 7., Appendix 5.4.1., for the plots of the residuals from the initial global model and Figure 8., for the plots of the residuals from the final model.

5.4.2. *Betula pendula* twig litter bags

It was not possible to retrieve all the litter bags set out, 56/60, 54/60, 55/60, 55/60, were found after 6, 12, 18 and 24 months, respectively (plots: D5EB, H5ZB, DFA1, DFA6, HFA6 and H4 contained missing values). For all treatments and sites decomposition rates were

fastest during the first 6 months see Figure 5.4.2. and Table 1., Appendix 5.4.2., for the decay constants.

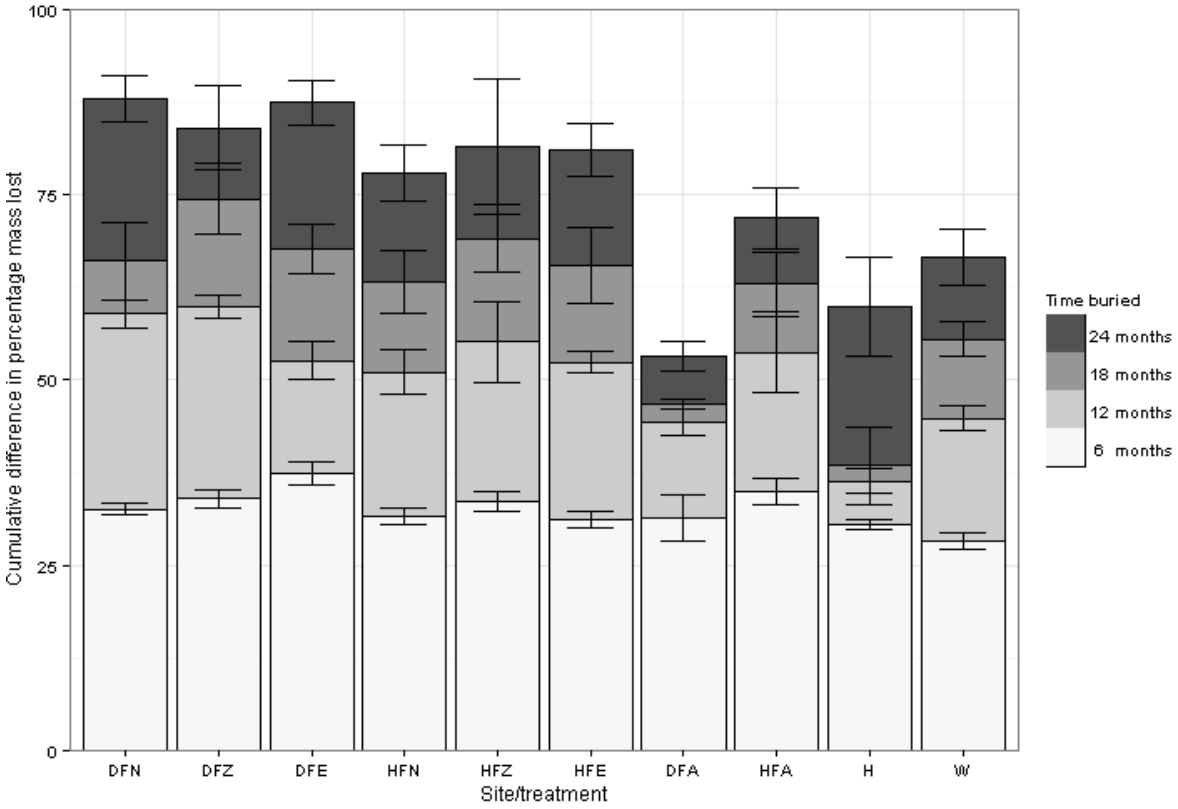

Figure 5.4.2. Cumulative difference in percentage dry mass lost of *B. pendula* twig litter bags after 6, 12, 18 and 24 month under each of the site/treatments (DFN = Deer's Farm Native, DFZ = Deer's Farm Near native, DFE = Deer's Farm Exotic, HFN = Howard's Field Native, HFZ = Howard's Field Near native, HFE = Howard's Field Exotic, DFA = Deer's Farm Adjacent, HFA = Howard's Field Adjacent, H = Wisley Common, W = Buxton Wood).

5.4.2.1. RHS experimental plots

A GLM found that percentage dry mass lost of the *B. pendula* twig litter bags was associated with the length of time buried ($F_{3, 132} = 298.26$, $p < 0.001$) and was significantly different between the two RHS experimental sites ($F_{1, 132} = 10.11$, $p < 0.01$), see Table 5.4.2.1.. Neither the vegetation origin treatment, nor planting mix, nor pH were found to significantly affect the percentage dry mass lost, these factors were removed during the stepwise deletion of non-significant terms; H0 was accepted. See Figure 1., Appendix 5.4.2., for the plots of the residuals from the final global model.

Table 5.4.2.1. Significant factors remaining in the *B. pendula* twig litter bag decomposition model: Adjusted R^2 = 1, AIC = 944.19, error: 132 d.f..

Term		d.f.	F value	p value	
Months buried	(6, 12,18 or 24)	3	298.26	p < 2.2 e-16	***
Site	(DF or HF)	1	10.11	p = 0.0018	**

NS: p > 0.05, *: p < 0.05, **: p < 0.01, ***: p < 0.001

See Figures 5.4.2.1. and 5.4.2.2. for linear regressions of the percentage dry mass remaining over time for the three vegetation origin treatments at Deer's Farm and Howard's Field, respectively. See Table 2., Appendix 5.4.2., for the R^2 and p values, as well as the decay gradients and Figures 2. and 3., Appendix 5.4.2., for graphs showing the linear regressions for each plot at Deer's Farm and Howard's Field, respectively. Second order polynomials do provide a good fit for the decomposition dataset, see Table 3. Appendix 5.4.2..

A glm of the decomposition rates also found no association with the vegetation origin treatment, planting mix or pH. In the decomposition rate models site (Deer's Farm or Howard's Field) had no significant effect on the decomposition rates, see Figure 4., Appendix 5.4.2., for the plots of the residuals from the final model.

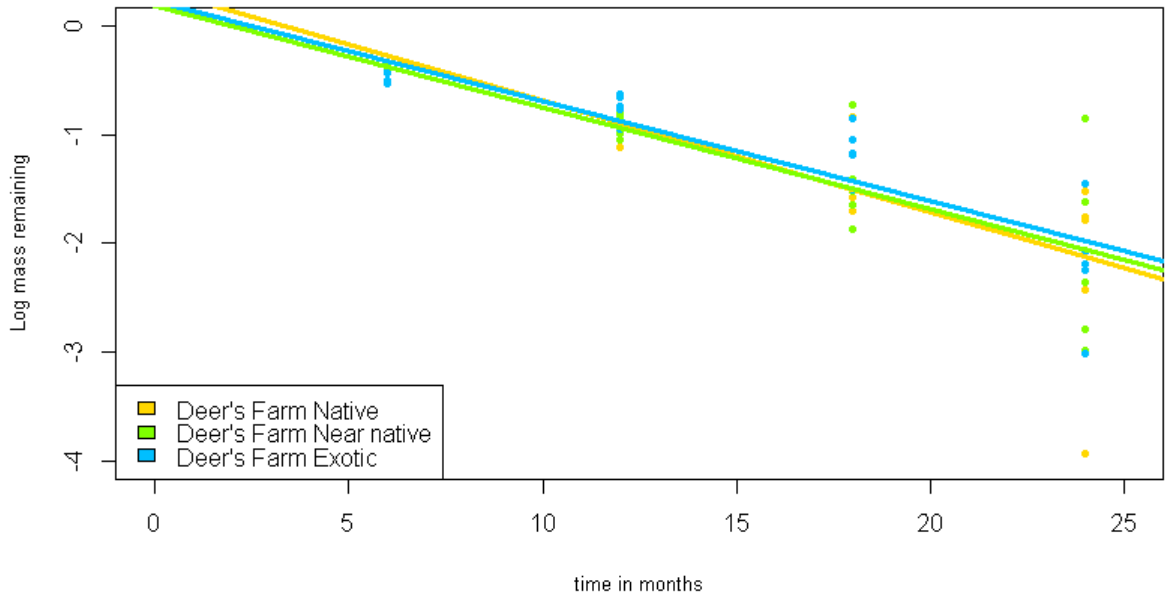

Figure 5.4.2.1. Linear regression of Log (percentage dry mass remaining/100) of *B. pendula* twig litter bags after 6, 12, 18 and 24 months under the three vegetation origin treatments at the Deer's Farm RHS experimental site. Native: yellow, Near native: green, Exotic: blue. See Table 2., Appendix 5.4.2. for the R^2, adjusted R^2 and p values.

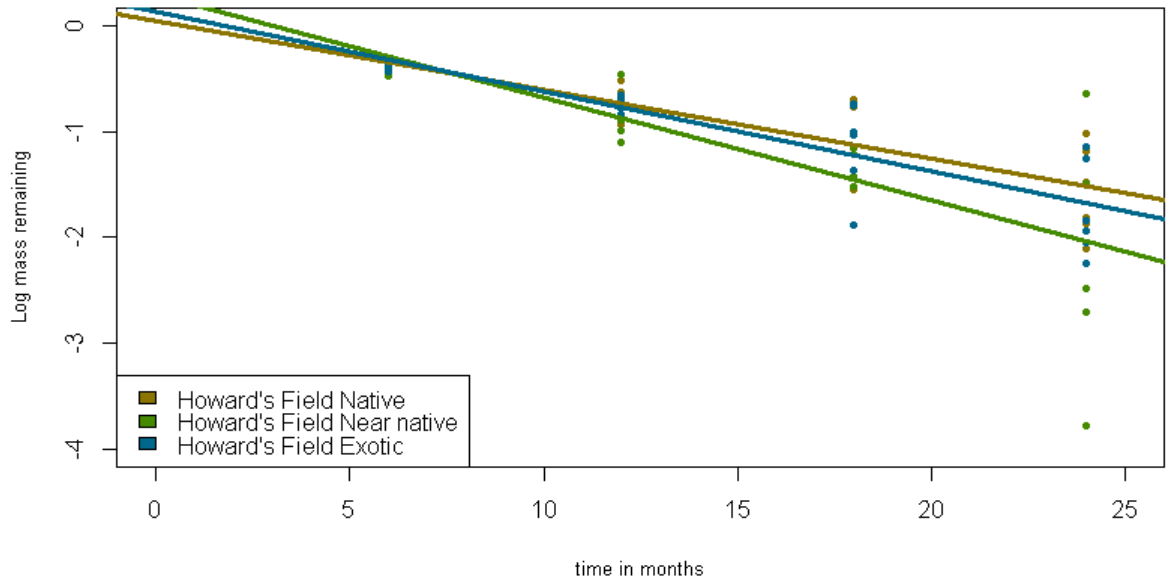

Figure 5.4.2.2. Linear regression of Log (percentage dry mass remaining/100) of *B. pendula* twig litter bags after 6, 12, 18 and 24 months under the three vegetation origin treatments at the Howard's Field RHS experimental site. Native: yellow, Near native: green, Exotic: blue. See Table 2., Appendix 5.4.2. for the R^2 and p values.

5.4.2.2. RHS experimental plots and adjacent grassland

A glm of the decomposition rates found that habitat (RHS experimental plot or adjacent grassland) had a significant effect on decomposition rates ($F_{1, 41} = 14.41$, $p < 0.001$), the decomposition rates were lower in the grassland, see Figure 5.4.2.3.. The other factors included in the starting model (site: Deer's Farm/Howard's Field, pH and interactions) were removed during step-wise deletion of non-significant terms. See Figure 5., Appendix 5.4.2., for the plots of the residuals from the final model.

5.4.2.3. All sites

A glm of the decomposition rates of the data from all sites found that site (Deer's Farm RHS experimental plots, Deer's Farm adjacent, Howard's Field, RHS experimental plots, Howard's Field adjacent, Wisley Common, Buxton Wood) had a significant effect on decomposition rates ($F_{5, 49} = 6.85$, $p < 0.001$), see Figure 5.4.2.3.. Other factors included in the starting model were removed during step-wise deletion of non-significant terms. See Figure 6., Appendix 5.4.2., for the plots of the residuals from the final model.

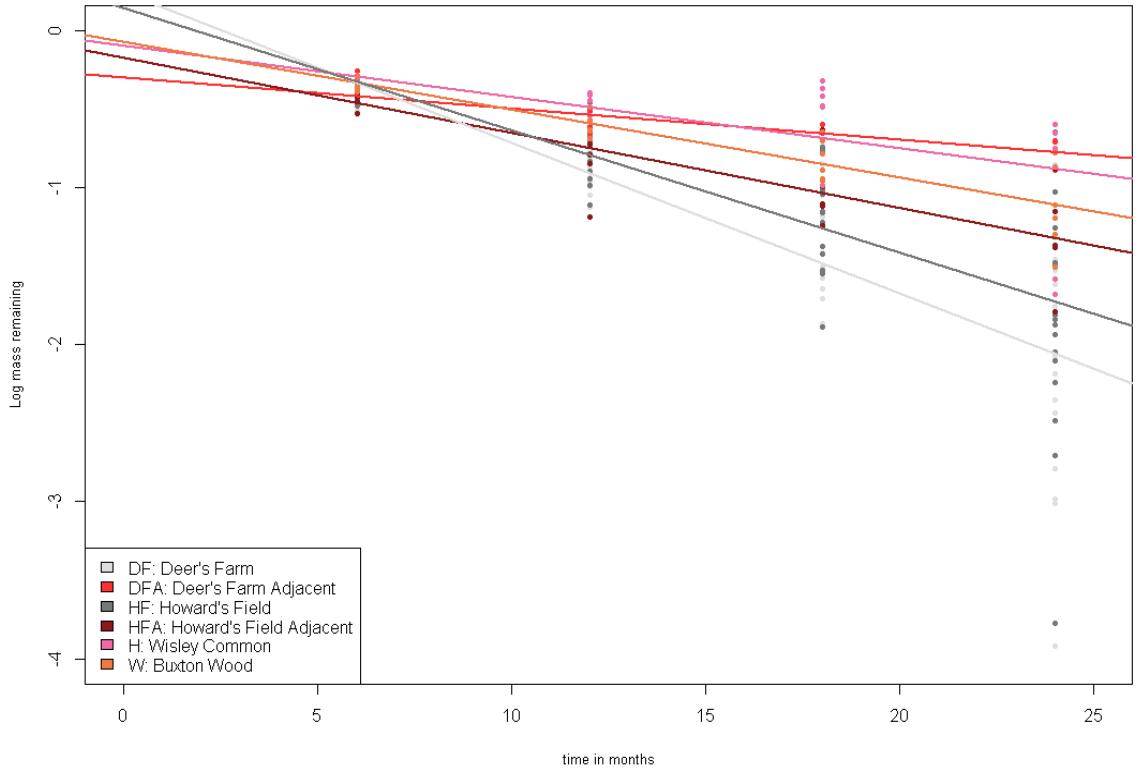

Figure 5.4.2.3. Linear regression of Log (percentage dry mass remaining/100) of *B. pendula* twig litter bags after 6, 12, 18 and 24 months at all sites. Deer's Farm RHS experimental plots: light grey, Deer's Farm Adjacent plots: light red, Howard's Field RHS experimental plots: dark grey, Howard's Field Adjacent plots: dark red, Wisley Common: pink, Buxton Wood: brown. See Table 2., Appendix 5.4.2. for the R^2 and p values.

Pearson's correlation coefficients were calculated to assess the association between the decomposition rates and the measurements of the soil property parameters from Chapter 2.. See Table 5.4.2.4. for the results where significant correlations were found and Figure 5.4.2.4. for graphs of plot mean pH, available magnesium, available phosphorus and available potassium plotted against the decomposition rates. Lower decomposition rates were found in the plots with lower pH and lower levels of available macronutrients.

Table 5.4.2.4. Soil parameters moderately to strongly correlated with *B. pendula* twig decomposition rate and whether these soil parameters were different between sites, see Chapter 2., Table 2.4. for results of Dunn's post-hoc tests showing between which sites the significant differences lay.

Soil parameter	r	d.f.	p value		Difference in parameter across sites (Chapter 2.)
pH	-0.573	53	p < 0.001	***	***
Mg	-0.600	53	p < 0.001	***	***
P	-0.325	53	p < 0.05	*	***
K	-0.444	53	p < 0.001	***	***

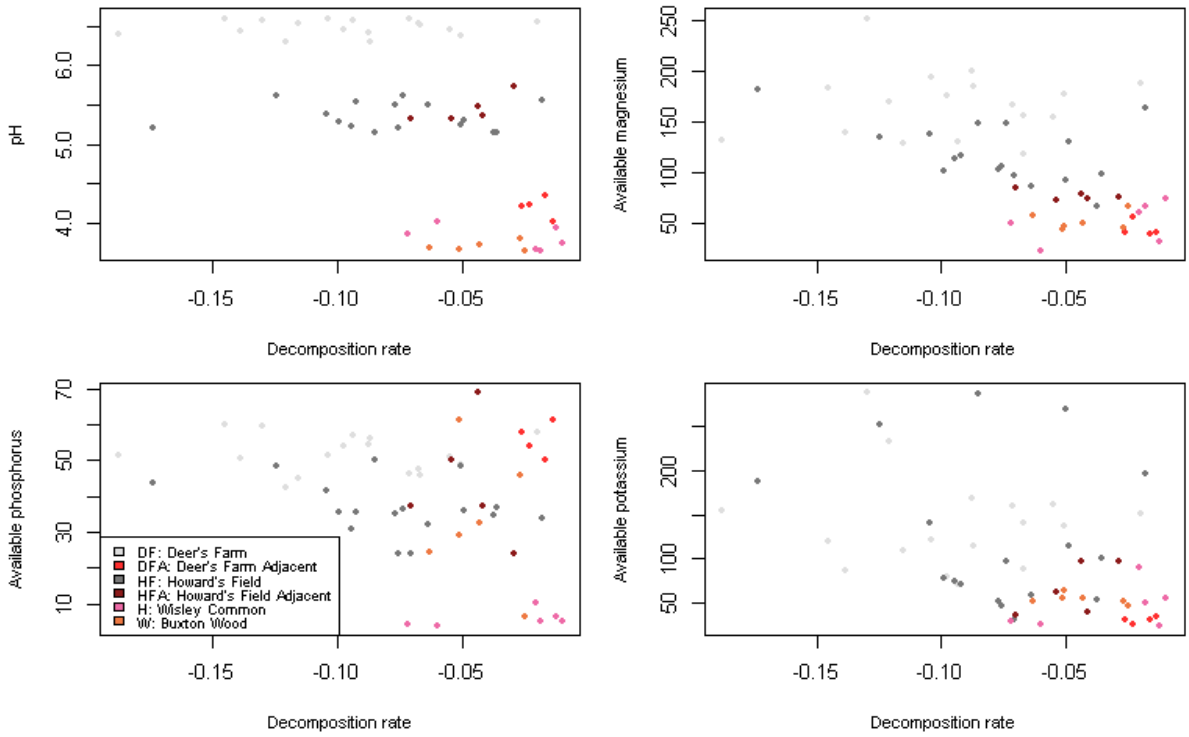

Figure 5.4.2.4. pH (top left), Mg (top right), P (bottom left), K (bottom right) against decomposition rates of *B. pendula* twig litter bags for all sites. Deer's Farm RHS experimental plots: light grey, Deer's Farm Adjacent plots: light red, Howard's Field RHS experimental plots: dark grey, Howard's Field Adjacent plots: dark red, Wisley Common: pink, Buxton Wood: brown. See Table 5.4.2.4. for the r and p values.

No significant correlations were found for total available nitrogen ($r = 0.119$, 53 d.f., $p > 0.05$), ammonium ($r = 0.224$, 53 d.f., $p > 0.05$) or nitrate ($r = 0.119$, 53 d.f., $p > 0.05$) separately, or LOI ($r = 0.093$, 53 d.f., $p > 0.05$).

5.4.3. Bait lamina strips

All bait lamina strips were retrieved. The data was 0 inflated especially for days 5 and 8, the first two recording occasions, where 28% and 17% of the plots did not record any feeding activity respectively, see Table 1., Appendix 5.4.3. for the mean percentage bait consumed per site/treatment for each day the strips were examined and Figure 5.4.3. for a cumulative stacked bar chart of the data for days 8, 14, 32 and 5, plotted with standard errors. See Table 2. Appendix 5.4.3. for the soil moisture content data included in the models.

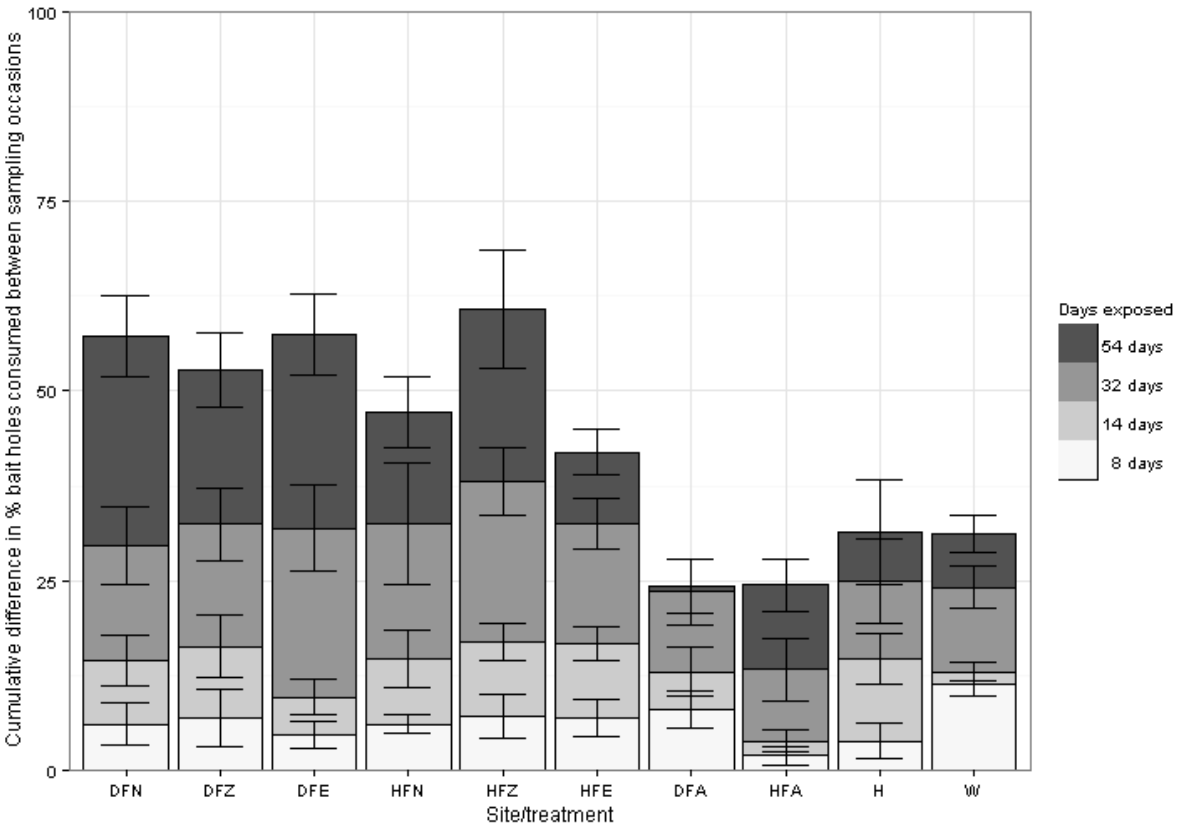

Figure 5.4.3. Cumulative difference in percentage of bait holes consumed after 8, 14, 32 and 54 days under each of the site/treatments (DFN = Deer's Farm Native, DFZ = Deer's Farm Near native, DFE = Deer's Farm Exotic, HFN = Howard's Field Native, HFZ = Howard's Field Near native, HFE = Howard's Field Exotic, DFA = Deer's Farm Adjacent, HFA = Howard's Field Adjacent, H = Wisley Common, W = Buxton Wood).

5.4.3.1. RHS experimental plots

Linear regression models were fitted, see Table 3., Appendix 5.4.3., adjusted R^2 and p values, as well as the bait consumption rates. See Figure 5.4.3.1. and Figure 5.4.3.2. for the linear regressions of each treatment (Native, Near native and Exotic) for Deer's Farm and Howard's Field, respectively and Figure 2. and 3., Appendix 5.4.3., for graphs showing the linear regressions for each plot.

A glm based on the bait consumption rates found that neither vegetation origin treatment, nor RHS experimental site, significantly affected the rate of bait consumption; H0 was accepted. Soil moisture, pH and all interaction terms were removed during the stepwise deletion of non-significant terms, until 'site' and 'treatment' remained in the final model, neither of which was significant ($F_{1, 32} = 0.76$, $p > 0.05$ and $F_{2, 32} = 0.66$, $p >$

0.05, respectively). See Figure 1., Appendix 5.4.3., for the plots of the residuals from the final model.

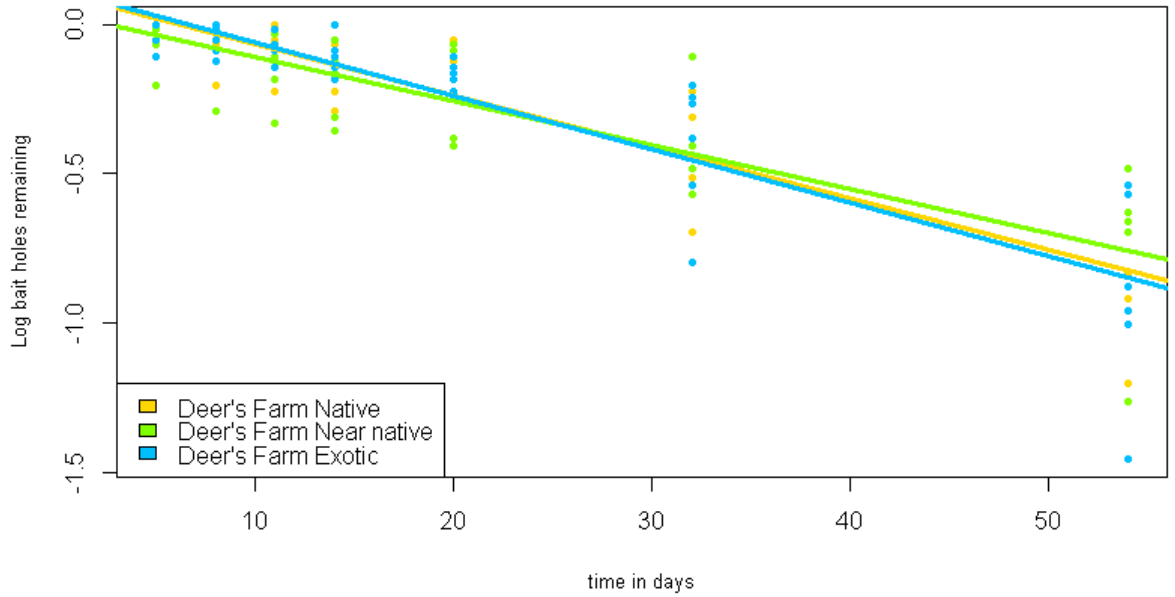

Figure 5.4.3.1. Linear regression of Log (percentage holes remaining filled/100) of bait lamina strips after 5, 8 ,11, 20, 32 and 54 days under the three vegetation origin treatments at the Deer's Farm RHS experimental site. Native: yellow, Near native: green, Exotic: blue. See Table 3., Appendix 5.4.3. for the R^2 and p values.

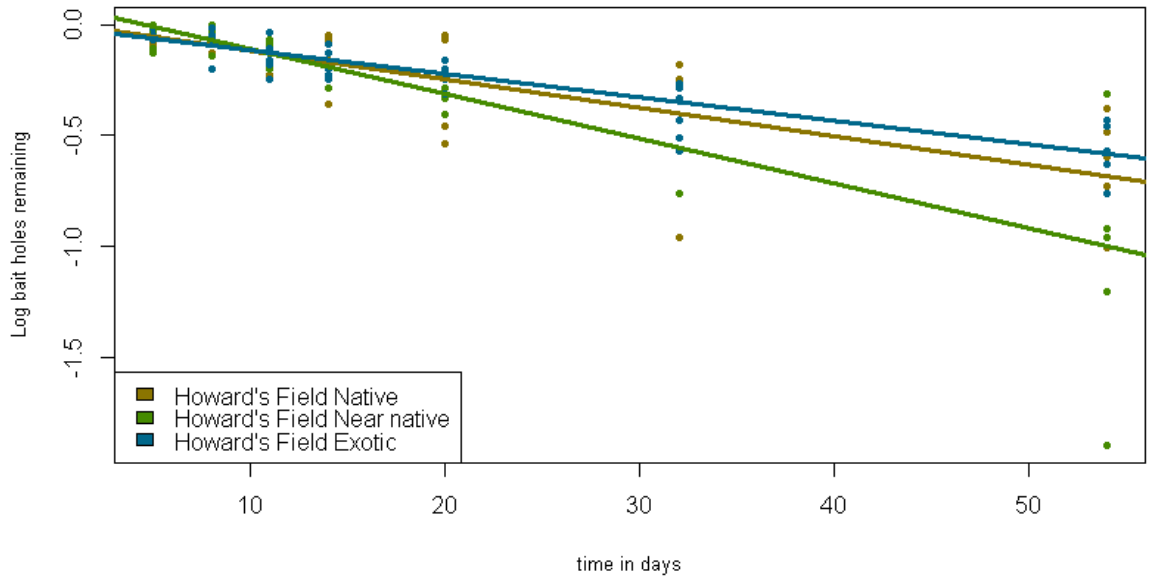

Figure 5.4.3.2. Linear regression of Log (percentage holes remaining filled/100) of bait lamina strips after 5, 8 ,11, 20, 32 and 54 days under the three vegetation origin treatments at the Howard's Field RHS experimental site. Native: yellow, Near native: green, Exotic: blue. See Table 3., Appendix 5.4.3. for the R^2 and p values.

5.4.3.2. RHS experimental plots and adjacent grassland.

A glm on the rate of bait consumption for the RHS experimental plots and their adjacent grassland found that site, soil moisture, pH and habitat were all significant factors, as well

as the interactions between site and soil moisture, and habitat and pH. See Table 5.4.3.2. for the associated p values and Figure 4. Appendix 5.4.3. for the plots of the residuals for the final model.

Table 5.4.3.2. Type III analysis of variance table for the significant terms in the RHS experimental plot and adjacent grassland bait consumption rate final model: Adjusted R^2 = 0.4507, AIC = -348.84, error: 41 d.f..

Term		d.f.	F value	p value	
Site	(DF or HF)	1	7.05	p = 0.011	*
Soil moisture		1	6.48	p = 0.015	*
pH		1	5.46	p = 0.024	*
Habitat	(RHS plot or grassland)	1	4.93	p = 0.032	*
Site: soil moisture	(interaction)	1	5.72	p = 0.021	*
Habitat: pH	(interaction)	1	5.52	p = 0.024	*

NS: p > 0.05, *: p < 0.05, **: p < 0.01, ***: p < 0.001

5.4.3.3. All sites

The linear regressions of bait consumption for each site (Deer's Farm, Deer's Farm Adjacent, Howard's Field, Howard's Field Adjacent, Wisley Common and Buxton Wood) are shown in Figure 5.4.3.3.. A glm on the rate of bait consumption across all the sites found that site was a significant factor ($F_{1, 54}$ = 8.50, p < 0.001). The interactions, soil moisture and pH were all removed during stepwise deletion of non-significant terms. In the penultimate model pH was the variable removed ($F_{1, 53}$ = 3.80, p = 0.056). See Table 5.4.3.3. for the p values of the final model (after pH was dropped) and Figure 5. Appendix 5.4.3. for the plots of the residuals.

Table 5.4.3.3. Type III analysis of variance table for the significant terms in the bait consumption rate final model for all sites: Adjusted R^2 = 0.388, AIC = -435.93.

Term	d.f.	Error d.f.	F value	p value	
Site	5	54	8.50	p = 5.59 e-6	***

NS: p > 0.05, *: p < 0.05, **: p < 0.01, ***: p < 0.001

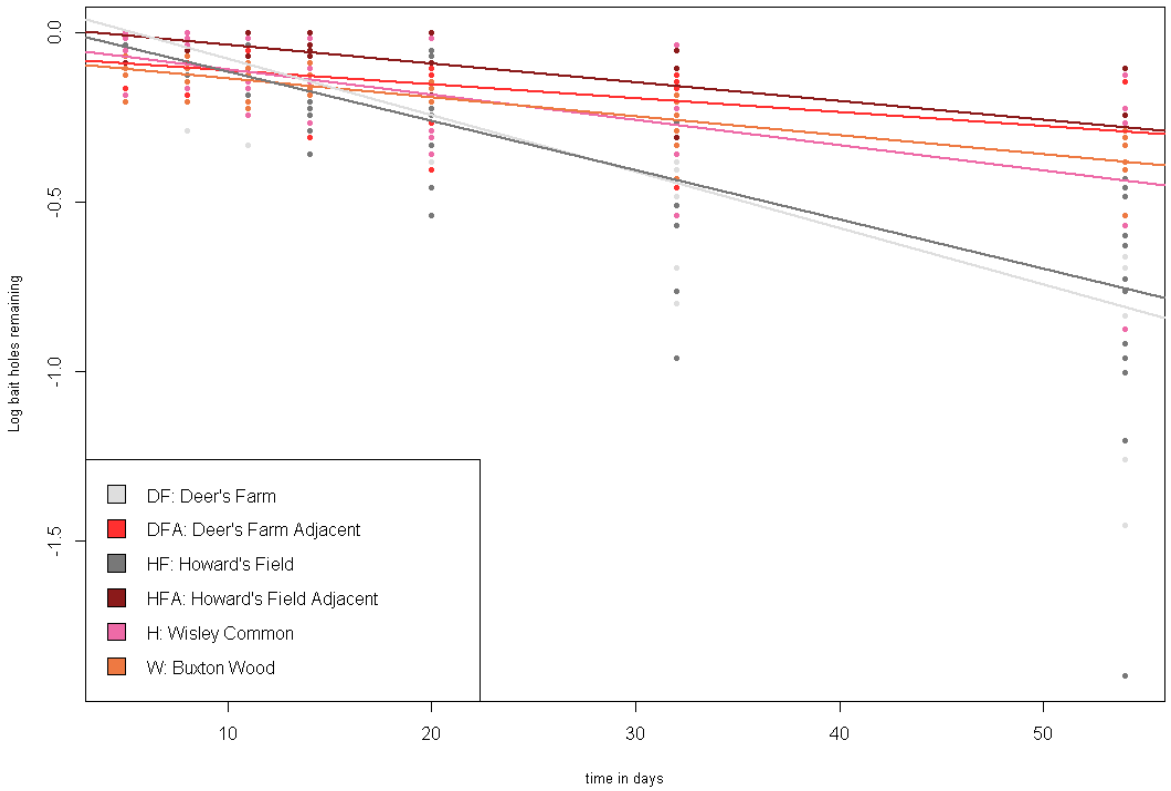

Figure 5.4.3.3. Linear regression of Log (percentage holes remaining filled/100) of bait lamina strips after 5, 8 ,11, 20, 32 and 54 days at all sites. Deer's Farm RHS experimental plots: light grey, Deer's Farm Adjacent plots: light red, Howard's Field RHS experimental plots: dark grey, Howard's Field Adjacent plots: dark red, Wisley Common: pink, Buxton Wood: brown. See Table 3., Appendix 5.4.3. for the R^2 and p values.

Across all sites there was a strong correlation between bait consumption and the depth of the bait: ($r = 0.839$, 148 d.f., $p < 0.001$), with the percentage of bait consumed being higher at lower depths, see Table 5.4.3.4. for separate correlations by site and Figure 5.4.3.4. for a plot of the linear regressions.

Table 5.4.3.4. Pearson's correlation coefficient of the percentage of bait lamina strip holes remaining filled under the different sites after 54 days.

Site		r	d.f.	p value	
Deer's Farm:	RHS experimental plots	0.955	43	p < 0.001	***
Deer's Farm:	Adjacent grassland	0.850	13	p < 0.001	***
Howard's Field:	RHS experimental plots	0.924	43	p < 0.001	***
Howard's Field:	Adjacent grassland	0.908	13	p < 0.001	***
Wisley Common		0.916	13	p < 0.001	***
Buxton Wood		0.929	13	p < 0.001	***

NS: p > 0.05, *: p < 0.05, **: p < 0.01, ***: p < 0.001

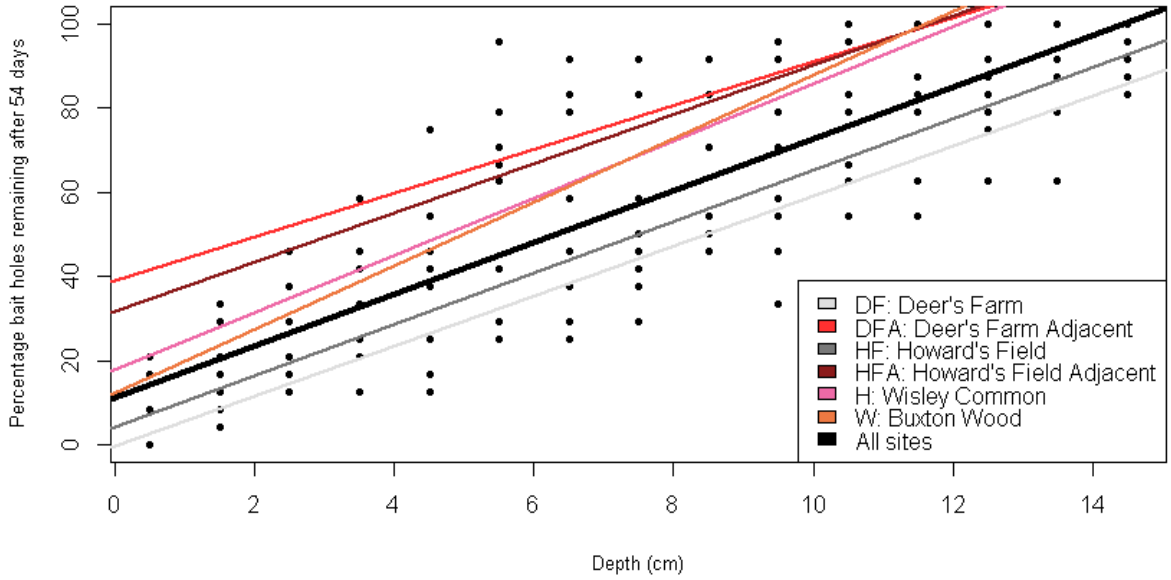

Figure 5.4.3.4. Linear regressions of percentage of holes with bait remaining at increasing depth after 54 days, for all sites. Deer's Farm RHS experimental plots: light grey, Deer's Farm Adjacent plots: light red, Howard's Field RHS experimental plots: dark grey, Howard's Field Adjacent plots: dark red, Wisley Common: pink, Buxton Wood: brown, all sites combined: black.

5.5. Discussion

5.5.1. Micro/Mesofauna decomposition

The role of the soil fauna in decomposition is key to nutrient cycling and ecosystem function as a whole. Here whether vegetation origin affects the decomposition processes is discussed. This research was designed so that it was possible to tease apart the decomposition functioning of the micro and mesofauna from that of the macrofauna. The size of the litter bag mesh used prevented earthworm litter access, so the leaf litter dry mass lost and the rates of decomposition of the twig litter is more likely to be due to the soil micro-organism and mesofauna activity, although it is only possible to discuss in relation to differences in abundance and diversity of the latter as that was the aspect explored in Chapters 3. and 4..

5.5.1.1. RHS experimental plots

There were no significant differences in *Q. robur* leaf litter percentage dry mass lost after exposure to decomposition processes for 6.5 months between the vegetation origin

treatments; Native, Near native or Exotic, at either the Deer's Farm or Howard's Field RHS experimental plots. These results are echoed for the *B. pendula* twig litter bags: the vegetation origin of the RHS experimental plots (Native, Near native, Exotic) was not found to influence the percentage dry mass lost or decomposition rates. There was also no difference between the two RHS study sites. This is an indication that the differences in Collembola abundance found between the vegetation origin treatments in Chapter 3., lower abundances in the Exotic plots, were not a limiting factor in the decomposition processes.

Oak leaf litter has been found to have relatively slow rates of decomposition compared to leaf litter of other tree species (Howard & Howard 1974). When comparing decomposition rates between species Howard and Howard (1974) found that for leaves of *Q. petraea* x *robur* under 40% of dry mass was lost after 700 days, here the leaves were exposed for 195 days with a mean percentage dry mass loss of 42.9% ± 3.3% and 41% ± 2.8% from the Deer's Farm and Howard's Field RHS experimental plots, respectively. These results indicate faster rates of decomposition within the RHS experimental plots and this is probably due, in part, to the leaf litter in the work of Howard and Howard (1974) being isolated in decomposition tubes which prevented access for the soil mesofauna as well as the soil macrofauna, but is still high compared to other more comparable studies. In Section 5.5.1.3. this will be referenced and discussed further when comparing the litter bag results across all sites.

5.5.1.2. RHS experimental plots and adjacent grassland

The percentage dry mass lost from the leaf litter bags buried in the RHS experimental plots was significantly greater than that lost from the leaf litter bags deployed in the

adjacent grassland. This was true for both the Deer's Farm and Howard's Field sites with these differences not being explained by pH in the final model. The same pattern was observed for the twig litter bags; the rates of decomposition were found to be faster in the RHS experimental plots than in the adjacent grassland, see Figures 5.4.1.3. and 5.4.2.. The percentage dry mass lost (*Q. robur* leaves) and decomposition rates (*B. pendula* twigs) were lowest in the grassland site adjacent to the Deer's Farm RHS experimental plots.

In Chapter 3. densities of both the Acari and Collembola were found to be higher in the adjacent grassland, with the species diversity indices indicating greater diversity of the latter also within the grassland, so it does not follow that greater abundance or diversity necessarily equates to higher decomposition rates and improved ecosystem function. However, there are a great many other factors that could be interacting and influencing these differences and in Chapter 3. the results did show that there was a significant dissimilarity in the Collembola communities found between the plots and grassland sites (Chapter 3., Figure 3.4.5.2. and Table 3.4.5.2.).

It could be that the soil fauna communities of the RHS experimental plots were better able break down the *Q. robur* leaves. Ciska Veen et al. (2014) found a 7.5% faster rate of decomposition where plant litter was in the vicinity of the plant from which it originated: the 'home-field advantage'. The grassland vegetation is more dissimilar to that of the parent material used in the bags and this could perhaps play a part in the higher decomposition rates observed in the RHS experimental plots compared to the adjacent grassland.

As discussed in Chapter 3. the vegetation structure and cover differed between the RHS experimental plots and the adjacent grassland (Table 3. Appendix 3.2.). Despite the litter bags being buried, the higher percentage of bare ground of the RHS experimental plots would have meant that the soil surface layer was more exposed relative to the other sites, see Chapter 3. Section 3.5.1.1. which could have resulted in in a differing soil microclimate. Vegetation affords ground cover and insulates against frost penetration, minimising physical disruption of the soil from abiotic factors (see Edwards and Cresser (1992) and references therein). The leaf litter bags were deployed from 24/9/12 to 11/4/13 and so were exposed to winter weather conditions, during which the exposure is likely to have been greater in the RHS experimental plots, potentially facilitating litter fragmentation and decomposition. The twig litter bags were set out from 21/12/11 to 26/12/13 and so were exposed to two winter periods, the differences in percentage dry mass lost between the sites were not correspondingly greater, but that may have been because decomposition is not a linear process (leaf litter bag percentage difference in mean dry mass loss between the RHS experimental plots and the adjacent grassland: 26.6%, and twig litter bag percentage difference in mean dry mass loss between the RHS experimental plots and the adjacent grassland: 19.6%).

There were also likely differences in soil structure between the habitats. Visually the soil of the Deer's Farm adjacent grassland site appeared more compacted than that of any of the other sites. A reduction in pore space could limit movement and access to the litter by the soil mesofauna hindering decomposition. However, if this had been the case, Chapter 3. would have found an associated decrease in Collembola abundance (Larsen et al. 2004), though to determine this with greater confidence it would have been necessary to separate the Collembola species based on life-form groups (epiedaphic, euedaphic and

hemiedaphic, see Chapter 1. Section 1.3.2.) as surface dwelling species, such as *C. thermophilus*, would not have been affected.

5.5.1.3. All sites

When all sites were considered, the percentage of dry mass lost from the *Q. robur* leaf litter bags was significantly different across all the sites, being greatest within the RHS experimental plots followed by Buxton Wood and lowest at the Deer's Farm adjacent grassland site (Section 5.4.1.3.). Decomposition rates of the *B. pendula* twigs were also significantly different across all the sites, with rates again being fastest within the RHS experimental plots and lowest at the Deer's Farm adjacent grassland site (with, in order, the Howard's Field adjacent grassland, Buxton Wood and Wisley Common sites with intermediate decomposition rates (see Figure 5.4.2.3. and Section 5.4.2.3.).

Pouyat and Carreiro (2003) found that leaf litter collected from both urban and rural areas decomposed faster at urban than in rural sites. Arguably the RHS experimental sites could be considered most similar to an urban area (certainly more so than either Wisley Common or Buxton Wood), in which case higher decomposition rates could have been expected. No information was provided as to the vegetation cover or microflora of the sites used by Pouyat and Carreiro (2003) and the factors proffered in explanation: the presence of exotic earthworm species and litter nitrogen content, were either not relevant or not measured in this study, respectively, in this study. So it is impossible to know whether the patterns of differences in decomposition observed here are brought about by the same causes.

Regarding 'home-field advantage', given the evidence that plant litter decomposes faster under the plant species it is derived from, it could have been expected that if any sites were to have facilitated decomposition and accelerated decay rates it would be those of Buxton Wood or possibly Wisley Common. Both *Q. robur* and *B. pendula* occurred at Buxton Wood whilst *B. pendula* saplings were frequent at Wisley Common, with young specimens being found within the 'plots'. Neither of these species were found at either the RHS experimental plot sites or their adjacent grassland, so the results of this study contradict the hypothesis somewhat, as the decomposition rates and percentage dry mass lost was highest in the RHS experimental plots. However, it could be that the decomposition of the RHS experimental plots is unusually high. Bocock and Gilbert (1957) used mesh bags exposed in a woodland (Roudsea Wood), also filled with *Q. robur* leaves, from December to June; so also six to seven months, and observed percentages of dry mass loss of 16.7% ± 1.24% to 17.4% ± 1.17% which are far lower than those found in the RHS experimental plots: 42.9% ± 3.3% and 41% ± 2.8% and are more similar to those of Buxton Wood: 27.67% ± 2.31% and Wisley Common: 22.01% ± 2.03%.

The soil property parameters measured in Chapter 2. were explored in relation to the *B. pendula* twig litter decomposition, as this was the litter bag data set it was possible to calculate decomposition rates for. Tree species have been found to alter the soil environmental conditions underneath their canopies, altering the ratios of available soil macronutrients with the resulting soil nitrogen, phosphorus and soil moisture properties found to be good predictors of *Quercus* species decomposition rates in previous studies (Aponte et al. 2012). It could have been expected that the soils with the higher total available nitrogen content (Buxton Wood) would have had higher decomposition rates as they are generally found to be more fertile, however, neither total N, nor the constituents

$NH4^+$ and $NO3^-$ were found to be correlated. Other parameters were correlated (Mg, P and K), but these were confounded with site, as can be seen from Figure 5.4.2.4. where the data points have been coloured to show which sites they were obtained from. pH was also found to be associated with decomposition rates; decreasing with increasing soil acidity. The twig litter starting general linear model included pH as a co-variate as there was variation within the 'habitat' RHS experimental plot and the 'habitat' adjacent grassland, and it is a factor often included in decomposition studies, but across all sites variation in decomposition rates was better accounted for by 'site' (Deer's Farm, Deer's Farm adjacent, Howard's Field, Howard's Field adjacent, Wisley Common and Buxton Wood), which encompasses all soil property and vegetation differences as a whole, than by pH alone.

One parameter that was not included was soil moisture; the leaf and twig litter bags were set out for 6.5 months and 24 months, respectively, so both sets were subject to seasonal fluctuations in soil moisture content. It would only have been possible to take point readings and calculate means, but unless these had been taken frequently enough, temporary changes would have been missed. Previous studies have shown that it is only at extremes that soil moisture has a greater effect than that of temperature upon soil respiration (a major component of which arises from the decomposition of litter) (e.g. Gabriel and Kellman (2014)). Soil moisture data was collected for the bait lamina strip assay as this study was of a shorter duration; 54 days.

5.5.2. Macrofaunal bait lamina decomposition

Literature indicates that bait lamina strip assays are an accurate representation of earthworm activity within the soil profile, (see Section 5.1.3.). Here bait consumption

increased with length of exposure, and decreased with increasing depth. Bait lamina consumption was found to be greatest in the upper levels of the soil profile, see Figure 5.4.3.4., supporting previous research (Hamel et al. 2007; Simpson et al. 2012; Geissen & Brümmer 1999) which also found evidence that feeding activity decreased with increasing soil depth. By day 54, across all sites, mean bait consumption was 92.5% and 83.3% for the top two holes, with feeding rates decreasing down to 9.2% of bait holes being perforated at the lowest depth; Simpson et al. (2012) also found highest activity in the top 2 cm. Although the earthworms were not sampled, from the literature the bait consumption observed here is likely due to the activity of epigeic and endogeic species of earthworms as anecic species tend to burrow and inhabit deeper levels of the soil profile (Bouché & Gardner 1984).

5.5.2.1. RHS experimental plots

There were no significant differences in the bait lamina consumption rates between the vegetation origin treatments; Native, Near native or Exotic, at either the Deer's Farm or Howard's Field RHS experimental plots. There was also no significant difference between the two RHS study sites. Neither pH nor soil moisture in the upper soil profile were found to be significantly associated with bait consumption rates in this study, although this may be because they were not at earthworm activity limiting levels, the importance of these parameters are discussed further in Section 5.5.2.2..

5.5.2.2. RHS experimental plots and adjacent grassland

For the comparison in earthworm activity between the RHS experimental plots and the adjacent grassland; site (Deer's Farm or Howard's Field), habitat (RHS experimental plot or adjacent grassland), pH and soil moisture were all found to be associated with bait

consumption rates. Higher rates of bait consumption were found at the RHS experimental plots than in the grassland and rates were higher at Deer's Farm than Howard's Field, bait consumption was positively associated with soil moisture content and pH, see Table 5.4.3.2.. This contrasts with the models focussing solely on the RHS experimental plots discussed above, however, across these sites and the adjacent grassland there was a greater range of soil moisture and pH values.

The soils of the study sites belong to the Bagshot beds soil formation, a free draining sandy loam, with a low pH (see Chapter 2., Section 2.1.). The mean pH values of the RHS experimental plots were found to be pH 6.5 and pH 5.4 for Deer's Farm and Howard's Field, respectively, whilst the soils of the adjacent grassland sites were: pH 4.2 and pH 5.4, for Deer's Farm adjacent and Howards Field adjacent, respectively (mean pH values derived from soil core samples (Roehampton analysis)). The pH of Howard's Field and its adjacent grassland was similar, though the Deer's Farm adjacent grassland was more acidic. Earthworms are known to be sensitive to pH with soil acidity often found to affect their distribution (Bocock & Gilbert, 1957; Edwards & Bohlen, 1996; Geissen & Brümmer, 1999; Gilbert & Bocock, 1960). Bocock and Gilbert set out coarse meshed litter bags, that permitted soil macrofauna access, at two sites: mull-humus (pH 5.6-6.3) and moder-humus (pH 3.2-4.7) (Gilbert & Bocock 1960). They found that 30% more dry mass was lost from litter bags at the site with the less acidic pH.

Although, differences in pH do not account for all of the differences observed in bait composition rates in this study, if they did then those of the Howard's Field RHS experimental plots and their adjacent grassland should be the same.

Soil moisture has also previously been found to be an important factor in decomposition studies, as it has been found to significantly affect earthworm activity (Simpson et al., 2012), with it being noted that dry soils '*are not a favourable habitat for earthworms, which are rarely or never found in arid and semiarid grasslands*' (Stanton 1988). Here soil moisture data was collected for the bait lamina strip aspect of the study each date the strips were assessed for activity. The soil moisture levels were found to be lower in the adjacent grassland, in units of percentage volumetric water content: mean of Deer's Farm adjacent 3.4 (compared to a mean of 7.8 for Deer's Farm RHS experimental) and a mean of 7.1 for Howard's Field adjacent (compared to 8.7 for Howard's Field RHS experimental) (see Table 2. Appendix 5.4.3.).

The greatest difference in bait lamina consumption between the sites was found for habitat; RHS experimental plot or adjacent grassland, and this could have been the result of soil compaction of the latter. Although compaction was not found to have affected the overall soil mesofauna abundances as Chapter 3. Sections 3.4.2. and 3.4.3. found higher Collembola and Acari densities in the adjacent grassland than the RHS experimental plots. It follows that compaction was unlikely to have affected their role in the decomposition process, however, earthworms are larger and soil compaction is known to have a detrimental impact on their activity and their contribution to ecosystem functioning (Lavelle et al., 2006; Turbé et al., 2010).

5.5.2.3. All sites

Consistent with the *Q. robur* leaf litter bag percentage dry mass loss results and the rates of *B. pendula* twig decomposition there was a significant difference in the rates of bait consumption across all sites, with the highest levels of activity found in the RHS

experimental plots (see Figure 5.4.3. and Figure 5.4.3.3.) and rates being particularly low in adjacent grassland sites. At all depths bait consumption rates were greatest in the RHS experimental plots (see Figure 5.4.3.4.). During stepwise deletion of non-significant terms pH was the last variable removed. There was a significant difference in pH across all the sites, see Chapter 2. (Section 2.4.1): the semi-natural habitats of Buxton Wood and Wisley Common were found to be the most acidic, with pH values ranging from pH 3.8 to pH 4.1 (mean pH 4.0) and pH 3.7 to pH 4.7 (mean pH 4.2), respectively, with both sites being significantly more acidic than both the RHS experimental plot sites and slightly more acidic than the adjacent grassland sites. As the bait consumption rates observed were higher at the wood and the heath sites than the grassland sites (despite having lower soil pH values), this would have caused pH to no-longer be significant within the models. It is highly likely that pH is still an important factor influencing earthworm presence and activity and it is probably the case that this indicates that there are additional factors (other than just pH) contributing to the lower rates observed at the grassland sites, for instance compaction.

Although differences in soil moisture between all sites were not found to significantly affect earthworm activity, soil moisture may still have had an impact, modulating feeding activity relating to depth. Soil moisture is often found to decrease with increasing depth and this could explain the observed patterns. Soil moisture data was collected at a constant depth and only on the dates the strips were checked for bait hole consumption, so it is not possible to determine if soil moisture and depth related feeding activity are correlated.

In the bait lamina study by Simpson et al. (2012), conducted at Wytham woods, Oxfordshire, after 34 days mean bait consumption was 8.5%. In this study bait consumption rates were greater; after 32 days mean bait consumption (across all depths and plots) at the Buxton Wood site was 24.2% and was 31.1% by the end of the study (day 54). The bait lamina strips used in this study were of a different design to those used by Simpson et al. (2012) who used strips of 16 apertures of 1.5 mm at 5 mm separations compared to 15 apertures of 2.5 mm at 1 cm intervals (5 mm separations were attempted but the PVC strips were found to be too brittle (Terrington, personal communication). This means that this study sampled to a greater depth, and as earthworm activity has been found to decrease with increasing depth the differences in earthworm activity are in fact greater than they at first appear. This provides further evidence that the decomposition processes/earthworm activity was unusually high in the RHS experimental plots and not that the rates encountered at the other sites were unusually low, just that they appeared low in comparison.

This difference between the rates observed by Simpson et al. (2012) and those observed at Buxton Wood is despite two factors that, according to the literature, should have resulted in lower bait consumption rates: the mean soil pH of their study site was higher although still the acidic side of neutral pH: 6.85 ± 0.51 and their strips were installed on the 19/09/09, which is during autumn when soil faunal activity is considered to be at its highest.

Bait lamina earthworm activity assays are not without limitations, data becomes less reliable with time; it has been suggested that the repeated pulling out of strips to check for perforation can knock the bait loose. However, as this is a comparative study and all

bait lamina strips were handled consistently this was not an issue within this study and the handling methodologies implemented in other studies were not markedly dissimilar. There were anomalies in bait consumption (between day 14 and day 20 under the Native treatment at the Deer's Farm site), although across the study these were minimal and this method remains the best available for assaying earthworm activity with the benefit of being comparatively nonintrusive.

5.5.3. Relationship to community structure and further work

The results of this study do support Bardgett's statement that there is evidence of redundancy in soil fauna communities regarding soil function (Bardgett 2002) and the common view that it is changes in soil community composition rather than purely species diversity that are of more importance when it comes to ecosystem functioning (Bardgett & van der Putten 2014). Wisley Common, Buxton Wood and the adjacent grassland sites had higher levels of species diversity and tended to have greater abundances of both Collembola and Acari, however, the percentage dry mass lost and decomposition rates were not correspondingly greater. It has been shown, though in a microcosm study, that functional dissimilarity between detritivorous species and not species richness has the greatest impact on decomposition (Heemsbergen et al. 2004).

Hedlund and Öhrn (2000) found that soil community respiration rates, another method of assessing ecosystem function, were significantly higher where three trophic levels (Fungi, Collembola and predatory mites) were included. These findings highlight the importance of interactions between the trophic levels for ecosystem functioning. This study only looked at the Collembola community at species level, a group of soil fauna which are known to only have an indirect impact on decomposition processes, ideally all soil fauna,

including (and especially) the bacteria, fungi and microfauna would have been investigated. Differences in these components between sites could potentially have mitigated the effects of the lower Collembola abundances and diversity encountered in the RHS experimental plots and may have led to the decomposition differences encountered between the different sites.

This chapter compared the decomposition processes for two native species (*Q. robur* and *B. pendula*) in native soils by native soil fauna. As already mentioned (Section 5.5.1.2.) it has been suggested recently that plant species have species specific decomposer communities, both in terms of the soil mesofauna community composition (Scheu et al. 2003) and the microbial community structure (McGuire & Treseder 2010). A natural progression for this work would be to explore the decomposition of exotic litter in garden habitats. Although this study found little evidence supporting the 'home-field advantage', according to that hypothesis it could be expected that exotic litter will decompose faster under more closely related plants or plants of the same species if their 'decomposer communities' are present; an extension of studies which look at native plants under a range of other native plants.

In gardens where exotic plants are grown perhaps if there are any differences in decomposition rates they are more likely to be the result of specific chemical properties of the litter generated by certain plants. Litter quality and properties are likely to differ. In the study by Aerts (1997) mass loss rates were associated with the lignin:N ratio in the plants of both the Mediterranean and tropical regions. Litter chemistry could have a greater impact on decomposition processes than vegetation origin per se; the plant species that litter is derived from directly affects the decay rates (Aponte et al. 2012),

though litter type has been found to be of decreasing importance in the late stages of decomposition (Aponte et al. 2012).

Further work could look at incorporating the species diversity metrics (Chapter 3.) into the models for the decomposition data for all sites. Chapter 3. suggested that there was a vegetation origin effect on soil fauna abundances (Acari and Collembola), but overall none was found for species diversity (Collembola) and in this chapter there was also no difference in decomposition rates between the treatments. However, there was a difference in both Collembola species diversity and community composition across all the sites and there were also difference found across all sites for both the decomposition data (*Q. robur* and *B. pendula*) and for earthworm feeding activity.

5.6. Conclusions

Vegetation origin had no effect on the decomposition of either *Q. robur* leaves or *B. pendula* twigs or on earthworm activity as assessed by rates of bait consumption, at either of the RHS experimental sites. The results indicate significant differences in decomposition rates across all sites, with those observed in the RHS experimental plots found to be consistently higher.

The impact of Collembola diversity could not be determined, as there was no between treatment/site difference in either the Collembola diversity for the RHS experimental plot vegetation origin treatments (from Chapters 3. and 4.) or the litter bag decomposition documented here.

As was found for Chapter 3. the RHS experimental plots were significantly different from the grassland sites immediately adjacent to them. From Chapter 3. soil mesofauna densities were found to be lower in the RHS experimental plots than in the adjacent grassland sites and Collembola species diversity indices were lower at the two RHS experimental sites than all the other sites. The greater abundances and species diversity of the non-RHS experimental sites did not translate into faster rates of decomposition, implications of this for garden habitat management are discussed in Chapter 6..

Chapter 6. Discussion

6.1. Maximising garden soil biodiversity

This Chapter seeks to bring together an overview of the results presented in Chapters 3., 4. and 5. regarding soil faunal biodiversity and soil ecosystem function in relation to garden management, in particular the choice of vegetion origin for garden plantings: Native, Near native or Exotic. First the responses of soil biodiversity to the planting regime will be reviewed along with their implications for garden management and maximising soil biodiversity (Sections 6.1.1. and 6.1.2.). Then the differences in soil ecosystem functions between the different vegetation origin treatments will be explored (Section 6.2.) to contribute to the discussion concerning the overall recommendations for vegetation origin planting decisions (Section 6.3.). Section 6.4. outlines possible future work and Section 6.5. summarises the main conclusions.

6.1.1. Soil mesofauna

Collembola species richness and diversity, based on the taxonomic diversity indices calculated in Chapter 3., were found to be greater for the less managed sites: the adjacent grassland, Wisley Common and Buxton Wood, than for the RHS experimental garden sites. Figure 3.4.5.2. (Chapter 3.) shows distinct communities in each of the four habitats: garden flowerbed (RHS experimental plots), grassland, heath and woodland; the two RHS experimental plots were more similar to each other than to the grassland mere metres to the side. The management implication from this is that to maximise soil biodiversity, maximise habitat diversity. Although it is not feasible for a person with the average sized garden (estimated at 190m^2 (Davies et al. 2009)) to establish a woodland or a heathland, the adjacent grassland could represent a lawn, which is achievable.

However, even if there is only space or the will for the maintenance of a flowerbed this is still likely to have greater Collembola biodiversity than a concrete patio, decking or a building extension. Even if the latter was improved with the addition of a green roof, this would likely only offer partial mitigation as they have been found to support impoverished, species poor, soil microarthropod communities (Rumble & Gange 2013).

It is difficult to compare the species diversities found in this study directly to other research due to the differences in Collembola extraction efficiencies, differences in the taxonomic level the soil fauna are grouped at, analysis approach and, most importantly, sampling effort (it is likely that there are still Collembola species present at the study sites that were not retrieved during sampling, see Figure 3.4.5.1.). For example Fountain (2002) also used Tullgren funnels, but with larger soil cores, extracted for a longer period over four sampling occasions. It is likely that coverage of the Collembola communities was similar, but it is not certain; Fountain (2002) produced no taxon sampling curves. Fountain (2002) looked at five urban sites in Wolverhampton with differing levels of soil contamination, finding a range of 15 to 24 species per site. The highest species richness was found at the most contaminated site, however, that site also had the lowest species eveness; it was dominated by *I. palustris* (54%) and *P. notabilis* (24%). Here total species richness figures were similar to Fountain's sites for the RHS experimental sites when the treatments were assessed separately (see Table 3.4.5.1.). In terms of community structure the RHS plots were also dominated by *P. notabilis*, for each treatment this species accounted for 51-63% of the population. However, it is worth recalling that *P. notabilis* could be representing several cryptic species (Porco et al. 2012), this highlights the benefits of including both taxonomic and phylogenetic approaches in comparative ecological studies. The greatest species richness across both this and the study by

Fountain (2002) was found at Wisley Common, there the Collembola population was also more even; the dominant taxon was the pooled *F. quadrioculata* 'group' (*F. manolachei* and *F. quadrioculata*) which accounted for 49% of specimens. The work of Fountain (2002) also highlights the importance of previous land use and management for present Collembola biodiversity.

Acari species diversity between the different vegetation origin treatments was not assessed here, however, Acari abundances were significantly different between the Native, Near native and Exotic treatments, with numbers lowest in the Exotic plots. As for the Collembola abundance patterns, higher densities were generally observed at the grassland, heathland and woodland sites than for the RHS experimental plots, but abundances are not necessarily indicative of biodiversity.

6.1.2. Implications for gardening management

This study did not find evidence of any significant difference between the Native, Near native and Exotic treatments, so regarding planting choice gardeners should look towards other selection criteria in order to maximise soil biodiversity. It is most likely that vegetation cover and structure are important parameters in encouraging garden biodiversity, including for the soil fauna. Previously garden vegetation cover has been found to be correlated with invertebrate abundance (Smith, 2006a) and the components of garden vegetation, specifically trees were found to be one of the most important factors in overall garden invertebrate species richness (Smith et al., 2006b). In this study, between the vegetation origin treatments, plant species richness was controlled. For invertebrate biodiversity the number of plant species grown is also important; increased plant species richness has been found to be positively related to arthropod species

richness (Siemann et al., 1998) and also Collembola density and diversity (Sabais et al. 2011). So a better approach for a gardener seeking to encourage biodiversity may lie in ensuring a wide selection of vegetation, as differences in Collembola diversity were found between the RHS experimental plots and the adjacent grassland this should also include a lawn type habitat.

As pH has been found to affect Acari abundances, both here and in agricultural situations; Siepel and Van de Bund (1988) found that the Acarina were adversely affected by fertiliser application, this has implications regarding garden management practices such as liming, which raises the soil pH. It is not new advice to suggest that pH altering chemicals should be applied with caution due to possible effects on soil organisms (e.g. (Griffith et al. 2002) who showed that liming removed waxcaps Hygrocybe from grassland flora). Evidence in the literature suggests that minimising activities that closely resemble tilling or that could result in soil compaction combined with a heterogeneous garden habitat approach and non-uniform application of lime or fertiliser could benefit soil biodiversity.

Another garden biodiversity consideration, not covered by this study, is pesticide use. Invertebrate pests still represent garden biodiversity, even if their presence is not desired. Insecticides/acaricides are often applied to treat pest species but they affect other components of arthropod communities and can have a significant impact on Collembola populations, both in terms of abundance and diversity (see Frampton, Gould, van den Brink and Hendy, (2007) and Frampton (2002), although their sampling strategies were more directed at hemiedaphic and epiedaphic Collembola species). Collembola are not often the target organism for pesticides; there are few Collembola that are considered

pest species, *Bourletiella hortensis* (one individual retrieved in this study) and *Sminthurus viridis*, the Lucerne 'Flea' (not retrieved here, although less likely to be as it is not an euedaphic species) being two occasional exceptions (Hopkin 1997). *Folsomia candida*, often used as a 'standard' test organism for estimating effects of pesticides on non-target arthropods, has been found to be sensitive to a range of organic chemicals (Fountain & Hopkin 2005), although soil invertebrates may be somewhat less exposed (Addison 1996).

6.2. Impacts of vegetation origin on soil ecosystem functions

Within the RHS experimental plots there was no difference in decomposition rates (litter bags and bait lamina consumption) between the vegetation origin treatments. This suggests that the ecosystem functioning does not differ between the treatments. The decay rates observed for the RHS experimental plots were faster than those of the semi-natural habitats and adjacent grassland sites.

In Chapter 5. the decomposition of native litter (*Quercus robur* and *Betula pendula*) was explored under differing vegetation origin treatments from habitats similar to those of suburban gardens, to semi-natural habitats: Buxton Wood and Wisley Common. The leaf and twig litter quality was native and in each case belonged to the same species so that sufficient quantities could be obtained and quality could be controlled as much as possible, as several parameters have been shown to influence decomposition rates (e.g. nitrogen, lignin, phenol and tannin content (Smith & Bradford 2003; Loranger et al. 2002; Aerts 1997; Melillo et al. 1982)). However, leaf litter origin has also been found to affect decomposition rates; leaves collected from urban areas were found to decompose faster due to alterations in litter quality (Dorendorf et al,2015). In this study all litter was collected from the same patch of woodland, however, this does have implications for

ecosystem function in urban areas, especially when the findings of Pouyat and Carreiro (2003) are also considered (overall faster decomposition rates in urban areas). In reality it will frequently be exotic plants producing litter in most urban to suburban locations.

The near native and exotic plants will be producing litter of an unknown and possibly variable quality. If decomposition rates are indeed higher in urban areas (e.g. because of their increased N content, see Pouyat and Carreiro (2003)) this could compensate for any vegetation origin litter quality alterations (e.g. increased lignin) that could slow down decomposition rates. It could be possible, however, to make decomposition rate probability predictions based on evolutionary history or leaf functional traits of the non-native plant species (see Cornelissen et al., (1999)).

6.3. Does it matter if you plant exotic plants in your garden?

Although differences were found in the abundances of the Collembola and the Acari between the vegetation origin treatments, Chapter 3. and Chapter 4. found no overall differences in Collembola diversity and Chapter 5. found that there was no significant difference in the ecosystem functioning as measured by decomposition across all vegetation origin treatments.

Soil biodiversity is not the only aspect of garden biodiversity, although until now it has been largely overlooked, other components should be included when making planting decisions. With regards to insect pollinators the 'Plants for Bugs' project found that although all vegetation origin treatments provided a resource for pollinating insects, that the assemblages of Native and Near native plants attracted the greatest abundances of pollinating insects (Salisbury et al., 2015). This supports Smith et al., (2006a) who found

solitary bee and hover fly abundance to be positively correlated with native plant species richness, with no correlation found for exotic plant species richness. It was also noted that more positively exotic plants can potentially, depending on species selected, extend the flowering season thereby prolonging resource availability (Salisbury et al., 2015).

Certain plants attract certain insects or are associated with particular taxonomic or functional groups of arthropods. For example *Chrysolina graminis* (Tansy beetle) is associated exclusively with the native plant *Tanacetum vulgare* (Tansy) (Chapman et al., 2006) which is also a herbaceous perennial on the RHS perfect for pollinators plant list (RHS 2011). So gardeners could also take this kind of specific species information into consideration when making planting decisions, though fewer associations of this kind are known about for the soil fauna.

However, as discussed in Chapter 3., Section 3.5.2.1. the Exotic and Near native plants, despite not directly impacting on native soil biodiversity, could be having indirect effects. They may be serving as vectors, facilitating the introduction and spread of their associated fauna, which would then have the potential to become naturalised and possibly invasive (Liebhold et al., 2012; Manchester & Bullock, 2000 cite Ward pers. comm.; Smith et al., 2007).

Probably a greater threat to UK biodiversity (floral) could arise from these introduced plant species escaping the confines of gardens and hybridising with (e.g. *Hyacinthoides* × *massartiana* (Rix 2004)) or out competing native plants and altering the vegetation structure of established habitats, e.g. *Impatiens glandulifera* (Himalayam balsam) (Centre for Aquatic Plant Management 2004)).

6.4. Further work

6.4.1. Soil fauna taxonomic diversity

As discussed in Section 3.5.1.1., vegetation cover was observed to vary with season and could be useful in explaining the significant differences in Acari and Collembola abundances between the vegetation origin treatments. Unfortunately the dates the vegetation cover was assessed did not correspond with four out of the six soil core sampling occasions; these data were collected as a separate aspect of the 'Plants for Bugs' project not covered here. However, for April '12 and October '12, as the soil core sampling co-ordinates are known and vegetation cover data for these months are available, it could be possible to go back and find out the vegetation cover for the point in the plot the core was collected from and incorporate this into a reduced model. Future work should consider vegetation cover as a co-variate and could look at any resulting differences in microclimate. If the differences in Collembola abundance/diversity are due to differences in vegetation cover and microclimate at the soil surface perhaps gardeners could also be advised not to 'weed' their flowerbeds, this would increase the cover afforded to bare ground, sheltering the soil surface (additionally increasing floral species richness).

In this study the species diversity of the Collembola were explored, with the only other group where sufficient numbers were retrieved being the Acari. Given enough time, expertise and identification keys it could be possible to identify all the Acari collected. However, this would be very laborious; over 3.5 times as many Acari were collected as Collembola, they are on average smaller and there was a large proportion of juvenile individuals. Instead the soil fauna could be studied in terms of functional groups, which

would minimise the depth of Acari identifications, whilst other taxa could be ascribed without specimen re-examination.

The Collembola could also be separated into the life-form groups: epiedaphic, hemiedaphic and euedaphic, as from looking at the species positions in the ordination diagram (Chapter 3., Figure 3.4.5.2.) and also the phylogram (Chapter 4., Figure 4.4.4.) it appears that some species groups prefer some habitats/soil properties over others, e.g. it looks like the adjacent grassland sites had fewer euedaphic species (for example: *Paratullbergia callipygos* and *Protaphorura armata* 'group' species.

6.4.2. Soil fauna phylogenetic diversity

In addition to the further work outlined in Chapter 4. Section 4.5.3., which covered *P. notabilis* lineages, the species designation of *S. reticulatus* and alternative sequence data collection and analysis methodologies, there is further work that could be undertaken.

As for Chapter 3. the phylogenetic diversity chapter (Chapter 4.) focussed on the Collembola, as in addition to the considerations outlined in Chapter 1. Section 1.3.2., this enabled comparison to the results of Chapter 3.. However, for the RHS experimental plot vegetation origin treatments this could be expanded to look at other taxonomic groups present or the whole soil mesofauna community found in the October '12 sampling occasion. This would be very difficult to achieve; it would require the identification to species level of all individuals retrieved for the sampling occasion although a high throughput sequencing platform e.g. the Roche/454 FLX (Margulies et al. 2005) could be utilised. High throughput sequencing would also be the required approach if the soil

microflora phylogenetic diversity were to be assessed although for this additional samples would need to be collected.

A more attainable extension of the work conducted for the analysis of phylogenetic diversity between the vegetation origin treatments in Chapter 4. would be to extend the work to cover the sampling occasions for the other seasons, as partially discussed in Section 4.5.3., considering the majority of Collembola have already been identified to the species level. It would still require a reasonable amount more molecular lab work, or/and the downloading and processing of sequences already available on GenBank, and might not add anything to the discussion of whether or not vegetation origin does impact Collembola diversity, especially as the phylogenetic diversity was found to be strongly positively correlated with the taxonomic diversity which already suggests no difference between planting treatments.

6.4.3. Soil fauna decomposition

No decomposition rate differences were found between the vegetation origin treatments applied in this study, but there were differences between the sites. As an extension of the work here it should be possible to look at the soil fauna abundance data and the Collembola diversity data in relation to the between site differences in the rates of decomposition. This would require that the unprocessed samples from Chapter 3., Section 3.2.2. be sorted, counted (Acari and Collembola) and identified (Collembola) to ensure a valid comparison for the adjacent grassland. Abundances would then be calculable per plot and comparable between October ’11 and April ’13. To enable a valid comparison of the species diversity metrics, the sampling effort of the RHS experimental sites should be reduced by two thirds, or separated into the different vegetation origin

treatments. This would be interesting as at the moment the results suggest that despite the RHS experimental plots having lower Collembola diversity they have higher decomposition rates. This data could also be assessed in terms of the functional groups present for all taxa (as contrasting functional attributes have been found to strongly affect decomposition processes (Heemsbergen et al. 2004) and also the Collembola and Acari tend to only have indirect impacts on decomposition processes), related to the vegetation cover/structure or the microflora abundance/diversity explored.

This study looked at the decomposition of two native tree species (*Quercus robur* and *Betula pendula*) under differing vegetation origin treatments, but as discussed in Chapter 5., Section 5.5.3. and here in Section 6.2. the decomposition of exotic plant matter in native soils should also be explored, as that is the vegetation that would be produced should non-native vegetation be grown.

6.5. Conclusions

The assumption that native garden plants are always best for biodiversity and that exotic species are inherently 'bad' has not found justification here. From this research it has been established that the vegetation origin (Native, Near native, Exotic) does not have a significant effect on either taxonomic or phylogenetic Collembola diversity or knock on effects on decomposition processes.

This work has added to the knowledge of Collembola species habitat preferences and has provided a record of the rare Collembola species *Willemia intermedia*, doubling the number of confirmed records (Hopkin 2007). A record and photographic documentation for the newly discovered, as yet undescribed, exotic *Katianna* species were also obtained;

prior to this only three specimens had been collected (Ardron 2009). The photos are now available on the Collembola checklist of the world (Janssens 2014). As this species was retrieved during the October ’12 sampling occasion, which was used for the molecular work, a COI barcode was also obtained. In total COI sequences were obtained for 25 species for which, as of June 2015, data had not been published on GenBank.

6.5.1. The impact of native and exotic plants on soil biodiversity

6.5.1.1. Abundance

Differences in both Collembola and Acari abundances were found between the RHS experimental plot vegetation origin treatments (Sections 3.5.1.1. and 3.5.1.2., respectively). The highest levels were found under the Native treatment, with the lowest levels in the Exotic plots though far greater differences in soil fauna densities were encountered between the RHS experimental plots and their adjacent grassland.

6.5.1.2. Taxonomic diversity

The Collembola were the component for which taxonomic diversity was assessed at the species level. There was a greater difference in Collembola species diversity, assessed by the diversity indices H’ and 1-D, between the two RHS experimental sites than between the vegetation origin treatments. There was no statistically significant difference in the diversity indices calculated between the vegetation origin treatments (Section 3.5.2.1.) and the Collembola communities encountered were less diverse from the RHS experimental plots than those of the adjacent grassland, Wisley Common and Buxton Wood (Section 3.5.2.2.).

6.5.1.3. Phylogenetic diversity

The results of the Collembola phylogenetic analysis performed on the October '12 subset of data in Chapter 4. agreed with the taxonomic diversity indices calculated in Chapter 3., in that there was no significant difference in Collembola phylogenetic diversity between the vegetation origin treatments.

6.5.2. The impact of native and exotic plants on ecosystem function

6.5.2.1. Decomposition processes

Vegetation origin had no effect on the decomposition of either *Q. robur* leaves or *B. pendula* twigs or on earthworm activity as assessed by rates of bait consumption (Sections 5.4.1.1. and 5.4.2.1.). As was found for Chapter 3. the main differences were found between the different sites, here decomposition processes were quicker at the RHS experimental plots than at the adjacent grassland sites, Wisley Common or Buxton Wood (see Sections 5.4.1.2., 5.4.1.3. 5.4.2.2. and 5.4.2.3. for the results and Sections 5.5.1.2., 5.5.1.3., 5.5.2.2. and 5.5.2.3. for a discussion of these apparently anomalous results).

6.5.2.2. Relationship with soil fauna

It was not possible to relate the Collembola diversity data from Chapters 3. or 4., to the decomposition, as both these chapters found that there was no difference between treatments and no difference was observed between the decomposition rates or percentage of dry mass lost. Differences were found between the RHS experimental plots and all the other additional sites for both the soil mesofauna communities (Collembola and Acari abundance, Collembola taxonomic diversity) and decomposition processes, but it was not within the scope of this project to try and relate, however, to achieve this the further work outlined in Section 6.4.3. could be undertaken.

6.5.3. Summary of implications, from this study, for gardeners

If gardeners are serious about maximising soil biodiversity in the UK their priority should be lobbying for the preservation of heath and woodland sites, and possibly other less managed habitats. Within the confines of their gardens they should seek to create a heterogeneously structured habitat with a variety of vegetation, ideally with at least the contrast of a flowerbed and a lawn. This work suggests that the vegetation origin 'Native', 'Near native' or 'Exotic' is not of paramount importance for soil biodiversity at least.

Appendix 1.5.2.

Table 1. Common diversity indices

Index		Equation
Shannon-Wiener index/ Shannon entropy	H	$H = -\sum_{i=1}^{S} p_i \log_b p_i$
Shannon equitability index	H'	$H' = -\sum_{i=1}^{S} p_i \log_e p_i$
Simpson index	D	$D = 1 - \sum_{i=1}^{S} p_i^2$
Gini-Simpson index	1-D	$1 - D$

* Where i = 1 … N (number of species), p_i is the proportion of the i^{th} species, and the log was originally calculated as log base 2.

Appendix 2.1.

Table 1. Deer's Farm (DF) and Howard's Field (HF) adjacent vascular plant species list.

Family	Species	Common name	DF adjacent	HF adjacent
Asteraceae	*Achillea millefolium*	Yarrow		X
Asteraceae	*Bellis perennis*	Daisy		X
Asteraceae	*Centaurea nigra*	Common knapweed		X
Asteraceae	*Hypochaeris radicata*	Cats ear	X	X
Asteraceae	*Leontodon hispidus*	Rough hawksbit		X
Asteraceae	*Senecio vulgaris*	Common groundsel		X
Asteraceae	*Taraxacum officionale agg.*	Dandelion		X
Caryophyllaceae	*Cerastium glomeratum*	Sticky mouse-ear chickweed	X	
Caryophyllaceae	*Cerastium semidecandrum*	Little mouse-ear chickweed	X	X
Caryophyllaceae	*Stellaria graminea*	Grassleaf starwort		X
Fabaceae	*Medicago lupulina*	Black medic		X
Fabaceae	*Ornithopus purpucillus*	Bird's foot trefoil	X	X
Fabaceae	*Trifolium arvense*	Haresfoot clover		X
Fabaceae	*Trifolium pratense*	Red clover		X
Fabaceae	*Trifolium repens*	White clover		X
Fabaceae	*Vicia sativa*	Common vetch		X
Geraniaceae	*Erodium cicutarium*	Common storksbill	X	
Geraniaceae	*Geranium molle*	Dovesfoot cranesbill	X	
Juncaceae	*Luzula campestris*	Field woodrush	X	X
Plantaginaceae	*Plantago lanceolata*	Ribbed plantain	X	X
Plantaginaceae	*Veronica arvensis*	Common speedwell	X	X
Plantaginaceae	*Veronica chamaedrys*	Germander speedwell		X
Poaceae	*Agrostis capillaris*	Common bent grass	X	X
Poaceae	*Anthoxanthum odoratum*	Sweet vernal grass		X
Poaceae	*Festuca ovina*	Sheep fescue	X	X
Poaceae	*Festuca rubra*	Red fescue		X
Poaceae	*Holcus lanatus*	Yorkshire fog		X
Poaceae	*Lolium perenne*	Perennial ryegrass		X
Poaceae	*Phleum pratense*	Timothy grass		X
Poaceae	*Poa annua*	Annual meadow grass		X
Poaceae	*Poa pratensis*	Smooth meadow grass	X	X
Polygonacaeae	*Rumex acetosella*	Sheeps sorrel		X
Portulacaceae	*Montia fontana*	Water brickweed		X
Ranunculaceae	*Ranunculus bulbosus*	Bulbous buttercup		X
Ranunculaceae	*Ranunculus repens*	Creeping buttercup		X
Rosaceae	*Aphanes australis*	Slender parsley-piert		X

Table 2. Deer's Farm (DF) and Howard's Field (HF) adjacent non-vascular plant species list.

	Species	Common name	DF adjacent	HF adjacent
Bryophyte	*Brachythecium rutabulum*	Rough stalked feather moss	X	
Bryophyte	*Bryum argenteum*	Silver green bryum moss	X	X
Bryophyte	*Homalothecium lutescens*	Yellow feather moss	X	X
Bryophyte	*Rhytidiadelphus squarrosus*	Springy lawn moss	X	X

Table 3. Wisley Common vascular plant species list.

Family	Species	Common name	Wisley Common
Aquifoliaceae	*Ilex aquifolium*	Holly	X
Asteraceae	*Cirsium vulgare*	Spear thistle	X
Asteraceae	*Senecio vulgaris*	Common groundsel	X
Betulacea	*Betula pendula*	Silver birch	X
Caryophyllaceae	*Cerastium glomeratum*	Sticky mouse-ear chickweed	X
Caryophyllaceae	*Stellaria media*	Common chickweed	X
Cyperaceae	*Carex pilulifera*	Pill sedge	X
Ericaceae	*Calluna vulgaris*	Ling	X
Ericaceae	*Erica tetralix*	Cross-leaved heather	X
Fabaceae	*Trifolium repens*	White clover	X
Fabaceae	*Ulex europaeus*	Common gorse	X
Fabaceae	*Ulex minor*	Dwarf gorse	X
Fagaceae	*Quercus rubra*	Red oak	X
Geraniaceae	*Erodium cicutarium*	Common storksbill	X
Geraniaceae	*Geranium molle*	Dovesfoot cranesbill	X
Juncaceae	*Juncus effusus*	Soft rush	X
Juncaceae	*Luzula multiflora*	Heath woodrush	X
Lamiaceae	*Teucrium scorodonia*	Woodland germander	X
Onagraceae	*Epilobium angustifolium*	Rosebay willowherb	X
Pinaceae	*Pinus sylvestris*	Scots pine	X
Poaceae	*Deschampsia flexuosa*	Wavy hair grass	X
Poaceae	*Molinia caerulea*	Purple moor grass	X
Polygonacaeae	*Plantago major*	Great plantain	X
Polygonacaeae	*Rumex acetosella*	Sheeps sorrel	X
Pteridophyte	*Pteridium aquilinum*	Bracken	X
Rosaceae	*Potentilla erecta*	Tormentil	X
Urticaceae	*Urtica dioica*	Stinging nettle	X

Table 4. Wisley Common non-vascular plant and lichen species list.

	Species	Common name	Wisley Common
Bryophyte	*Aulacomnium androgynum*	Drumsticks	X
Bryophyte	*Brachythecium rutabulum*	Rough stalked feather moss	X
Bryophyte	*Bryum argenteum*	Silver green bryum moss	X
Bryophyte	*Campylopus fragilis*	Brittle swan-neck moss	X
Bryophyte	*Campylopus introflexus*	Heath star moss	X
Bryophyte	*Dicranoweisia cirrata*	Common pincushion	X
Bryophyte	*Dicranum scoparium*	Broom moss	X
Bryophyte	*Hypnum jutlandicum*	Heath plait-moss	X
Bryophyte	*Polytrichum juniperinum*	Juniper haircap moss	X
Bryophyte	*Pseudoscleropodium purum*	Neat feather moss	X
Bryophyte	*Sphagnum capillifolium*	Red bog moss	X
Lichen	*Cladonia coniocraea*	NA	X
Lichen	*Cladonia portentosa*	Reindeer lichen	X
Lichen	*Cladonia pyxidata*	Pixie cups	X

Table 5. Buxton Wood vascular plant species list.

Family	Species	Common name	Buxton Wood
Adoxaceae	*Sambucus nigra*	Elderberry	X
Asparagaceae	*Hyacinthoides non-scripta*	Bluebell	X
Betulacea	*Betula pendula*	Silver birch	X
Fagaceae	*Fagus sylvatica*	Beech	X
Fagaceae	*Quercus robur*	English oak	X
Lamiaceae	*Teucrium scorodonia*	Woodland germander	X
Pinaceae	*Larix decidua*	European larch	X
Pinaceae	*Pinus nigra*	European black pine	X
Polygonacaeae	*Rumex acetosella*	Sheeps sorrel	X
Pteridophyte	*Pteridium aquilinum*	Bracken	X
Rosaceae	*Rubus fruticosus agg.*	Brambles	X
Rubiaceae	*Galium aparine*	Stickyweed	X

Table 6. Buxton Wood non-vascular plant species list.

	Species	Common name	Buxton Wood
Bryophyte	*Brachythecium rutabulum*	Rough stalked feather moss	X
Bryophyte	*Campylopus introflexus*	Heath star moss	X
Bryophyte	*Hypnum cupressiforme*	Cypress-leaved plait-moss	X
Bryophyte	*Kindbergia praelonga*	Common feather-moss	X
Bryophyte	*Mnium hornum*	Carpet moss	X
Bryophyte	*Polytrichastrum formosum*	Bank haircap	X

Appendix 2.2.

Table 1. Plant species used in the RHS experimental plots.

Treatment	Group	Species	Common name
Native	A B C	*Armeria maritima*	Sea thrift
	A B C	*Buxus sempervirens*	Common box
	A B	*Cytisus scoparius*	Common broom
	A	*Deschampsia cespitosa*	Tufted hair grass
	B C	*Dianthus deltoides*	Maiden pink
	B	*Dryopteris filix-mas*	Male fern
	B C	*Eupatorium cannabinum*	Hemp agrimony
	A B	*Geranium sanguineum*	Bloody cranesbill
	C	*Helianthemum nummularium*	Common rockrose
	A C	*Hyacinthoides nonscripta*	English bluebell
	B	*Knautia arvensis*	Field scabious
	A B C	*Leucanthemum vulgare*	Ox-eye daisy
	A B C	*Lonicera periclymenum*	'Graham Thomas' Common honeysuckle
	A B	*Lythrum salicaria*	Purple loosestrife
	B C	*Malva moschata*	Musk mallow
	C	*Molinia caerulea*	Purple moor grass
	A B	*Primula vulgaris*	Primrose
	B C	*Rosa rubiginosa*	Sweet briar
	A C	*Scabiosa columbaria*	Small scabious
	A C	*Stachys officinalis*	Betony
	A	*Valeriana officinalis*	Common valerian
	C	*Veronica spicata*	Spiked speedwell
	A	*Viburnum opulus*	Guelder rose
Near Native	A B C	*Armeria juniperifolia*	Juniper-leaved thrift
	C	*Calamagrostis brachytricha*	Korean feather reed grass
	B C	*Dianthus plumarius*	Cottage pink
	B	*Dryopteris wallichiana*	Alpine wood fern
	B C	*Eupatorium maculatum*	'Orchard Dene' Joe Pye weed
	A B	*Genista lydia*	Lydian broom
	A B	*Geranium macrorrhizum*	Bigroot cranesbill
	C	*Halimium umbellatum*	Umbel-flowered sun rose
	A C	*Hyacinthoides hispanica*	Spanish bluebell
	B	*Knautia macedonica*	Macedonican scabious
	A B C	*Lonicera tragophylla*	Chinese honeysuckle
	A B	*Lythrum virgatum*	'Dropmore Purple' wand loosestrife
	B C	*Malva alcea*	Greater musk mallow
	A B	*Primula japonica*	'Miller's Crimson' Japanese primrose
	A B C	*Rhodanthemum hosmariense*	Moroccan daisy
	B C	*Rosa rubrifolia*	Red-leaved rose
	A B C	*Sarcococca hookeriana* var. *humilis*	Christmas box, sweet box
	A C	*Scabiosa caucasica*	Caucasian scabious
	A C	*Stachys byzantina*	Lamb's ear
	A	*Stipa tenuissima*	Mexican feather grass
	A	*Valeriana phu* 'Aurea'	Golden valerian
	C	*Veronica austriaca* subsp. *teucrium*	Saw-leaved speedwell
	A	*Viburnum sargentii*	Sargent viburnum
Exotic	B C	*Acaena microphylla*	New Zealand burr
	B	*Alstroemeria psittacina*	Parrot lily
	A	*Azara serrata*	
	B	*Blechnum chilense*	Chilean hard fern
	C	*Brachyglottis monroi*	Monro's ragwort
	A B	*Callistemon rigidus*	Stiff bottlebrush
	C	*Carex testacea*	Orange New Zealand sedge

A	*Diascia personata* 'Hopleys'	Diascia 'Hopley's'
A B C	*Eccremocarpus scaber*	Chilean glory bower
A C	*Eryngium agavifolium*	Agave-leaved sea holly
A B C	*Euryops tysonii*	Euryops
B C	*Fuchsia magellanica*	Lady's eardrops
C	*Hebe rakaiensis*	Rakai hebe
A B	*Leptinella squalida*	Leptinella 'Platt's Black'
A C	*Lobelia tupa*	Devil's tobacco
A B	*Mirabilis jalapa*	Marvel of Peru, four o'clock flower
A C	*Nerine bowdenii*	Bowden Cornish lily
B C	*Osteospermum jucundum*	Boneseed
A B	*Oxalis adenophylla*	Sauer klee
A	*Ozothamnus rosmarinifolius* *	Sea rosemary
A B C	*Pittosporum tenuifolium*	Tawhiwhi
A B C	*Sisyrinchium striatum*	Pale yellow-eyed grass
A	*Uncinia rubra*	Red hook sedge
B C	*Verbena bonariensis*	Purple top

* replaced with *Azara* due to *Phytophthora* rot.

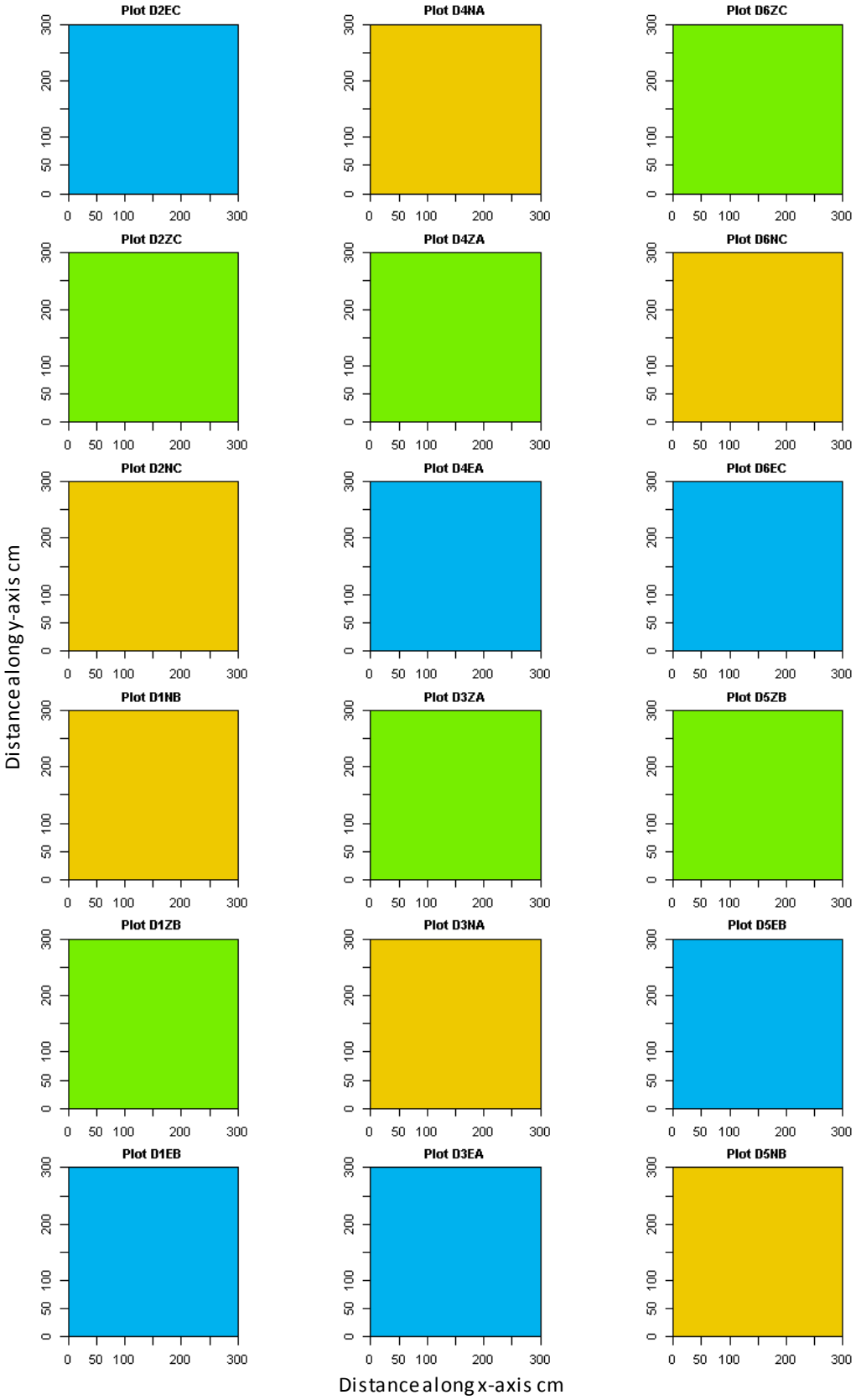

Figure 1. Deer's Farm RHS experimental plots: yellow = Native plots, green = Near native plots and blue = Exotic plots.

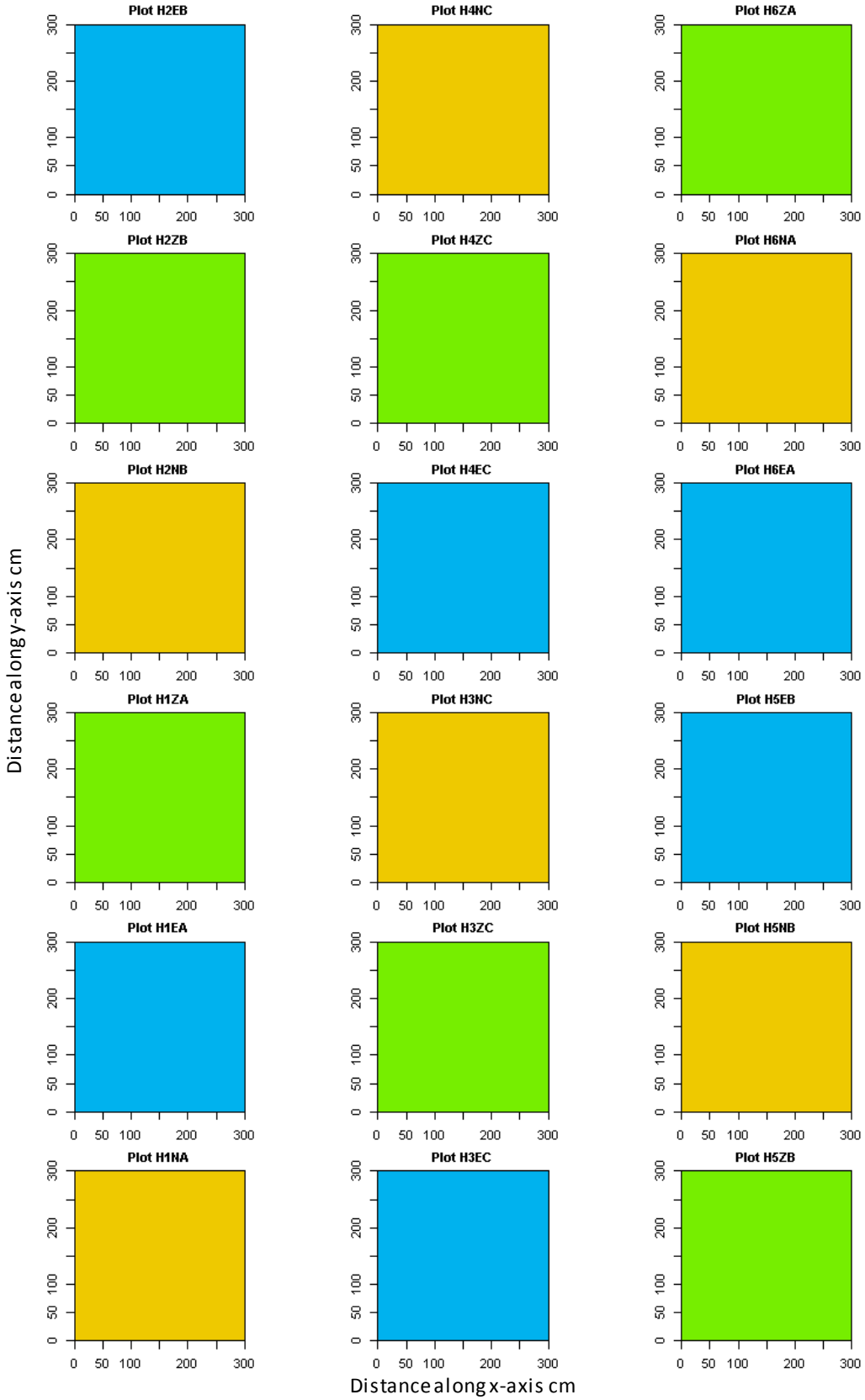

Figure 2. Howard's Field RHS experimental plots: yellow = Native plots, green = Near native plots and blue = Exotic plots.

Appendix 2.4.

Table 1. Soil pH (Roehampton analysis). N: Native, Z: Near native, E: Exotic, A: Adjacent.

		July' 11		Oct '11		Apr '12		July '12		Oct '12		Apr '13	
Site/treatment	**Plot**	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**
Deer's N	D5NB	6.36	6.07	6.35	6.15	6.94	6.32	6.38	6.38	6.03	6.31	6.46	5.92
	D3NA	6.12	6.41	6.03	6.35	7.07	6.55	6.53	6.32	6.35	6.51	6.41	6.13
	D1NB	6.14	6.34	6.22	6.39	7.15	6.52	6.54	6.52	6.28	6.40	6.60	6.49
	D2NC	6.36	6.48	6.32	6.41	7.45	6.68	6.73	6.74	6.35	6.64	6.44	6.51
	D6NC	6.33	6.44	6.00	6.39	7.21	6.34	6.74	6.61	6.39	6.74	6.66	6.60
	D4NA	6.25	6.45	6.15	6.53	7.12	6.63	6.59	6.67	6.52	6.57	6.56	6.30
Deer's Z	D1ZB	6.51	6.47	6.25	6.42	7.34	6.53	6.60	6.48	5.88	6.55	6.61	6.59
	D3ZA	6.43	6.51	6.31	6.42	7.20	6.73	6.73	6.64	6.48	6.60	6.57	6.63
	D5ZB	6.61	6.60	6.24	6.26	7.48	6.58	6.59	6.57	6.28	6.59	6.50	6.72
	D2ZC	6.37	6.73	6.34	6.24	7.14	6.32	6.84	6.62	6.11	6.62	6.65	6.62
	D4ZA	6.59	6.56	6.37	6.35	7.26	6.64	6.68	6.61	6.29	6.61	6.39	6.63
	D6ZC	6.59	6.61	6.34	6.45	7.28	6.78	6.56	6.40	6.61	6.67	6.43	6.55
Deer's E	D1EB	6.44	6.42	6.49	6.21	7.36	6.58	6.43	6.27	6.08	6.28	6.17	6.30
	D3EA	5.95	6.39	5.86	6.12	7.20	6.56	6.54	6.33	6.08	6.37	5.97	6.36
	D5EB	6.47	6.59	6.48	6.29	7.51	6.60	6.44	6.46	6.15	6.24	6.41	6.41
	D6EC	6.55	6.50	6.42	6.18	7.18	6.36	6.52	6.27	6.29	6.20	6.42	6.31
	D4EA	6.54	6.41	6.17	5.81	6.93	6.74	6.47	6.39	5.89	6.40	6.32	6.39
	D2EC	6.31	6.58	6.06	6.35	7.35	6.59	6.29	6.45	6.22	6.42	6.38	6.52
Howard's N	H1NA	5.36	5.22	5.49	5.01	5.87	5.41	5.97	5.59	5.55	6.03	5.46	4.98
	H5NB	5.53	5.14	5.29	5.78	5.95	5.55	6.29	5.53	5.69	5.71	5.57	5.45
	H3NC	5.10	5.46	5.01	5.13	5.31	5.46	5.24	5.04	4.60	5.10	5.17	5.27
	H2NB	5.18	5.38	5.29	4.93	5.37	5.33	5.23	5.10	4.89	4.65	5.03	5.35
	H6NA	5.43	5.28	5.02	5.33	5.56	5.62	5.29	5.19	4.90	5.29	5.56	5.54
	H4NC	5.40	5.42	5.20	5.18	5.38	5.58	5.55	5.48	5.24	4.68	5.47	5.14
Howard's Z	H5ZB	5.27	5.32	5.01	5.29	5.35	5.32	5.28	5.32	5.05	5.13	5.59	5.33
	H3ZC	5.42	5.38	5.00	5.36	5.50	5.62	5.31	5.69	5.47	5.02	5.91	4.95
	H1ZA	5.16	5.27	5.13	4.96	5.07	5.30	5.37	5.18	5.01	5.49	5.23	5.38
	H2ZB	5.40	6.04	5.29	5.28	5.87	5.74	5.30	5.60	5.68	5.04	5.81	5.76
	H4ZC	5.22	5.51	5.79	5.41	6.12	5.89	5.72	5.55	5.33	5.89	5.48	5.57
	H6ZA	5.53	5.82	5.11	5.41	5.51	5.88	5.52	5.45	5.70	5.06	5.48	5.55
Howard's E	H3EC	5.39	5.22	5.17	5.09	5.27	5.37	5.25	5.30	4.95	5.36	4.84	5.50
	H1EA	5.51	5.22	5.46	5.32	5.25	5.27	5.26	5.30	5.18	5.12	4.99	5.14
	H5EB	5.16	5.27	4.90	5.48	5.23	5.65	5.46	5.04	4.75	5.03	4.92	4.85
	H6EA	5.30	5.63	5.38	6.05	5.43	5.41	5.48	5.60	5.20	5.37	5.25	6.47
	H4EC	5.40	5.55	5.06	4.94	5.54	5.32	5.27	5.40	5.05	5.24	5.42	5.29
	H2EB	5.35	5.50	4.82	4.50	5.70	5.40	5.50	5.22	4.99	4.88	5.37	5.19
Deer's A	DA1	4.37	4.30	4.81	4.34	4.08	3.99	3.93	4.14	4.75	4.19	3.92	4.41
	DA2	4.62	4.29	5.07	4.71	4.12	4.06	4.01	4.28	4.70	4.40	4.01	4.12
	DA3	4.48	5.34	4.78	4.85	4.15	3.98	4.37	3.87	4.05	3.81	3.77	4.69
	DA4	4.32	4.62	5.58	5.04	3.88	3.94	3.96	3.96	3.96	4.04	3.79	4.03
	DA5	4.47	4.40	4.89	4.92	3.91	3.76	3.90	3.68	3.88	3.90	3.62	3.77
	DA6	3.86	3.81	4.74	4.87	3.84	3.88	3.68	3.69	3.76	3.96	3.79	3.65

Howard's A	HA1	5.07	5.34	4.18	6.08	5.83	5.95	5.44	5.88	3.96	3.91	6.19	5.78
	HA2	5.27	5.29	5.71	6.09	5.25	5.99	4.12	4.16	5.82	6.03	6.09	4.46
	HA3	5.06	5.42	4.82	6.15	6.13	6.24	6.27	5.68	5.97	6.00	5.84	4.29
	HA4	5.13	5.09	4.37	4.60	4.67	6.05	5.12	4.89	5.82	5.96	6.01	5.81
	HA5	5.39	5.47	5.68	5.62	6.17	5.85	6.17	4.38	5.40	5.21	5.19	5.20
	HA6	5.27	5.04	4.98	5.78	5.77	6.02	4.14	5.18	4.34	4.34	6.23	5.86
Wisley	H1	NA	NA	3.45	3.54	3.71	3.64	3.85	3.55	3.58	3.60	3.58	3.95
Common	H2	NA	NA	3.49	3.73	4.00	3.55	3.58	3.42	3.75	3.88	3.50	3.78
	H3	NA	NA	3.54	3.82	3.86	3.78	3.65	3.51	3.94	4.01	3.48	3.81
	H4	NA	NA	3.84	3.81	3.78	3.81	3.94	3.85	3.79	3.83	4.06	3.84
	H5	NA	NA	4.16	3.92	4.31	4.07	3.57	4.22	3.95	4.11	4.02	3.80
	H6	NA	NA	3.93	3.86	3.70	3.58	4.07	3.88	3.95	4.41	3.64	4.33
Buxton Wood	W1	NA	NA	3.51	3.58	3.70	3.70	3.62	3.51	3.82	3.80	3.73	3.62
	W2	NA	NA	3.51	3.56	3.66	3.65	3.60	3.49	3.71	3.98	3.66	3.57
	W3	NA	NA	3.50	3.44	3.76	3.67	3.79	3.61	3.64	3.70	3.91	3.60
	W4	NA	NA	3.74	3.52	3.81	3.66	3.49	4.05	3.83	3.91	3.67	3.56
	W5	NA	NA	3.52	3.46	4.09	3.91	3.62	3.44	3.99	4.14	3.64	4.15
	W6	NA	NA	3.65	3.47	3.69	3.59	3.63	3.77	3.77	3.89	3.70	3.66

Table 2. 2014 soil analysis results conducted by NRM laboratories. N: Native, Z: Near native, E: Exotic, A: Adjacent.

Site/ treatment	Plot	P index	K index	Mg Index	P available (mg/l)	K available (mg/l)	Mg available (mg/l)	LOI	pH	N available (Kg/ha)	Nitrate (mg/Kg)	Ammonium (mg/Kg)	Dry Matter (% w/w)
Deer's N	D5NB	3	2	3	42.6	233	170	6.4	7.9	20.8	2.25	2.94	81.6
	D3NA	4	-2	3	51.4	154	132	4.4	7.8	9.9	0.96	1.52	89.7
	D1NB	4	-2	3	50.8	162	155	5.5	8	13.0	1.71	1.55	83.7
	D2NC	4	-2	3	46.4	159	167	6.4	7.6	9.8	0.95	1.51	80.2
	D6NC	3	1	3	45.2	109	129	3.9	7.3	5.1	0.38	0.90	88.9
	D4NA	4	1	3	47.4	89	118	4	7.4	8.1	0.91	1.12	90.7
Deer's Z	D1ZB	4	-2	3	45.8	140	156	5.7	7.7	24.7	3.65	2.53	85.6
	D3ZA	4	1	4	60	120	184	5.9	7.4	11.9	1.80	1.17	91.8
	D5ZB	4	1	3	57.2	71	131	4.5	7.7	17.0	3.08	1.16	89.3
	D2ZC	4	-2	4	57.8	151	189	6.5	7.8	14.7	1.45	2.21	85.4
	D4ZA	4	3	5	59.6	288	253	8.2	7.7	63.8	12.92	3.04	92.3
	D6ZC	4	-2	4	51.4	121	194	7.3	7.7	16.3	2.25	1.82	87.2
Deer's E	D1EB	4	-2	4	54.6	169	201	6.2	7.6	32.9	6.74	1.49	90.8
	D3EA	4	1	4	56	114	185	5.9	7.8	22.9	4.65	1.08	93.1
	D5EB	4	1	4	56	92	185	6.2	7.3	22.9	4.65	1.08	92.3
	D6EC	4	1	3	50.6	87	139	4.3	7.7	10.2	1.11	1.45	90.8
	D4EA	4	-2	4	49	138	178	8.5	7.7	10.5	1.18	1.43	89.8
	D2EC	4	1	4	54	80	176	10.3	7.6	26.0	4.33	2.16	79.2
Howard's N	H1NA	3	0	3	35	53	103	6.5	6.1	8.3	0.83	1.25	91.0
	H5NB	3	1	3	36.6	98	148	6	5.9	13.5	1.72	1.66	81.5

	H3NC	3	1	2	37	100	99	4.5	6.2	17.3	1.99	2.33	83.7
	H2NB	4	3	3	50	286	148	5	6.7	42.7	9.04	1.64	88.1
	H6NA	2	0	2	23.8	31	97	5.4	6.1	9.8	0.87	1.58	84.2
	H4NC	3	1	3	36.2	115	131	8	5.8	23.0	3.19	2.55	84.3
Howard's Z	H5ZB	3	-2	3	45	133	135	5.7	6.4	17.0	2.43	1.82	79.8
	H3ZC	3	-2	3	41.4	141	138	5.9	5.9	9.0	1.14	1.10	91.6
	H1ZA	3	2	4	43.8	187	182	7.1	7	19.7	2.70	2.22	76.1
	H2ZB	3	2	3	33.8	196	164	9.4	6.6	22.6	3.77	1.89	78.4
	H4ZC	4	3	3	48.6	251	135	8.2	6.7	21.2	2.46	2.85	85.7
	H6ZA	3	0	2	32	59	87	5.9	6	13.2	1.68	1.62	87.2
Howard's E	H3EC	3	1	3	31	75	114	6.6	6.1	27.9	5.26	1.71	80.4
	H1EA	4	3	2	48.6	269	92	6.1	6.6	16.6	2.80	1.35	89.7
	H5EB	3	0	2	34.8	54	66	3.4	6.1	9.8	1.02	1.44	86.9
	H6EA	3	1	3	35.6	71	116	6.9	5.8	28.8	5.66	1.54	89.1
	H4EC	3	1	3	35.4	78	102	5.1	6.2	15.8	2.59	1.38	86.7
	H2EB	2	0	3	24	47	106	5.8	5.9	15.6	1.75	2.14	90.1
Deer's A	DA1	4	0	2	60.6	51	51	3.5	5	7.9	0.72	1.26	93.5
	DA2	4	0	1	50	31	39	2.7	4.8	14.0	2.38	1.12	86.8
	DA3	4	0	2	54	27	56	3.4	5.5	10.9	0.77	1.96	94.1
	DA4	4	0	1	57.8	32	40	3.5	4.8	15.3	0.89	2.93	95.5
	DA5	4	0	1	61.2	34	41	3.4	4.4	13.8	1.20	2.25	96.2
	DA6	4	0	1	61.4	44	49	3.5	4.8	10.7	0.42	2.24	94.4
Howard's A	HA1	3	0	2	37.4	37	85	4.4	7	16.1	1.08	2.94	82.8
	HA2	3	0	2	37.4	40	74	3.4	6.6	8.5	0.65	1.48	88.9
	HA3	2	1	2	23.8	98	76	4.3	5.1	15.8	2.44	1.50	93.4
	HA4	4	1	2	50	62	72	31	6.7	9.0	0.92	1.34	89.9
	HA5	4	1	2	69	97	78	3	6.1	7.9	0.76	1.22	91.1
	HA6	4	0	2	47.8	39	94	7	7.1	18.5	1.73	2.89	86.1
Wisley	H1	0	0	2	5.2	51	66	28.8	3.7	22.3	0.47	5.12	63.0
Common	H2	1	1	2	10.4	91	60	17	3.9	56.4	11.45	2.65	68.0
	H3	0	0	2	5	56	74	13.7	3.9	11.8	0.30	2.66	75.0
	H4	0	0	1	4.4	30	50	3.3	4.4	7.9	0.29	1.69	80.2
	H5	0	0	0	4	27	22	1.2	4.3	4.8	0.24	0.97	90.5
	H6	0	0	1	6.4	25	32	1.6	4.7	6.5	0.27	1.36	91.0
Buxton	W1	4	0	1	61.4	56	44	4	4	64.3	14.17	1.90	78.1
Wood	W2	0	0	2	6.4	47	67	45.2	3.8	158.6	33.84	5.79	40.7
	W3	3	1	1	29	65	46	6	4.1	43.8	8.83	2.11	69.0
	W4	3	0	1	32.4	56	49	8.2	4	44.9	9.23	1.98	69.5
	W5	4	0	1	45.8	52	45	3.9	4.1	38.5	7.19	2.44	77.1
	W6	2	0	2	24.4	52	57	6.5	4.1	26.4	3.50	3.09	70.0

Table 3. Dunn's post-hoc test results: Z statistics and p values for multiple comparisons of pH between sites. *'s denote results were there was a significant difference. DF: Deer's Farm RHS experimental plots, HF: Howard's Field RHS experimental plots, DFA: Deer's Farm adjacent, HFA: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood.

	W	DF	DFA	HF	HFA
DF	**Z = -5.51** **p < 0.0001 *** **				
DFA	**Z = -0.92** **p = 1**	**Z = 4.39** **p = 0.0001 *** **			
HF	**Z = -2.83** **p < 0.05 *** *	**Z = 3.8** **p < 0.01 *** **	**Z =-1.7** **p > 0.05**		
HFA	**Z = -2.72** **p < 0.05 *** *	**Z = 2.18** **p > 0.05**	**Z = -1.8** **p > 0.05**	**Z = -0.51** **p = 1**	
H	**Z = -0.09** **p = 1**	**Z = 5.4** **p < 0.0001 *** **	**Z = 0.83** **p = 1**	**Z = 2.72** **p < 0.05 *** *	**Z = 2.63** **p > 0.05**

Table 4. Paired T-tests comparing the average pH values obtained from the soil core analysis at Roehampton and the pH values obtained by NRM laboratories at each of the sites.

Site	degrees of freedom	t-value	p-value	
Deer's Farm	17	-19.55	p < 0.001	***
Howard's Field	17	-8.92	p < 0.001	***
Deer's Farm Adjacent	5	-4.33	p = 0.007	**
Howard's Field Adjacent	5	-3.12	p = 0.026	*
Wisley Common	5	-3.15	p = 0.025	*
Buxton Wood	5	-7.80	p < 0.001	***

Table 5. Dunn's post-hoc test results: Z statistics and p values for multiple comparisons of magnesium between sites. *'s denote results were there was a significant difference. DF: Deer's Farm RHS experimental plots, HF: Howard's Field RHS experimental plots, DFA: Deer's Farm adjacent, HFA: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood.

	W	DF	DFA	HF	HFA
DF	**Z = -4.70** **p < 0.0001 *** **				
DFA	**Z = 0.26** **p = 1**	**Z = 5.03** **p < 0.0001 *** **			
HF	**Z = -3.02** **p < 0.05 *** *	**Z = 2.38** **p > 0.05**	**Z =-3.34** **p < 0.01 *** **		
HFA	**Z = -1.2** **p = 1**	**Z = 3.24** **p < 0.01 *** **	**Z = -1.47** **p = 1**	**Z = 1.54** **p > 0.05**	
H	**Z = -0.05** **p = 1**	**Z = 4.63** **p < 0.0001 *** **	**Z = -0.32** **p = 1**	**Z = 2.95** **p < 0.05 *** *	**Z = 1.15** **p = 1**

Table 6. Dunn's post-hoc test results: Z statistics and p values for multiple comparisons of Phosphorus availability between sites. *'s denote results were there was a significant difference. DF: Deer's Farm RHS experimental plots, HF: Howard's Field RHS experimental plots, DFA: Deer's Farm adjacent, HFA: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood.

	W	DF	DFA	HF	HFA
DF	**Z = -2.52** **p > 0.05**				
DFA	**Z = -2.93** **p < 0.05 ***	**Z = -1.07** **p = 1**			
HF	**Z = 0.02** **p = 1**	**Z = 3.59** **p < 0.01 ****	**Z = 3.60** **p < 0.01 ****		
HFA	**Z = -0.98** **p = 1**	**Z = 1.32** **p = 1**	**Z = 1.95** **p > 0.05**	**Z = 1.21** **p = 1**	
H	**Z = 1.84** **p > 0.05**	**Z = 4.77** **p < 0.0001 *****	**Z = 4.76** **p < 0.0001 *****	**Z = 2.23** **p > 0.05**	**Z = 2.81** **p < 0.05 ***

Table 7. Dunn's post-hoc test results: Z statistics and p values for multiple comparisons of potassium availability between sites. *'s denote results were there was a significant difference. DF: Deer's Farm RHS experimental plots, HF: Howard's Field RHS experimental plots, DFA: Deer's Farm adjacent, HFA: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood.

	W	DF	DFA	HF	HFA
DF	**Z = -2.94** **p < 0.05 ***				
DFA	**Z = 1.12** **p = 1**	**Z = 4.31** **p = 0.0001 *****			
HF	**Z = -2.08** **p > 0. 05**	**Z = 1.22** **p = 1**	**Z = -3.45** **p < 0.01 ****		
HFA	**Z = -0.17** **p = 1**	**Z = 2.73** **p < 0.05 ***	**Z = -1.29** **p = 1**	**Z = 1.87** **p > 0.05**	
H	**Z = 0.65** **p = 1**	**Z = 3.74** **p < 0.01 ****	**Z = -0.47** **p = 1**	**Z = 2.88** **p < 0.05 ***	**Z = 0.82** **p = 1**

Table 8. Dunn's post-hoc test results: Z statistics and p values for multiple comparisons of Loss on ignition (LOI) between sites. *'s denote results were there was a significant difference. DF: Deer's Farm RHS experimental plots, HF: Howard's Field RHS experimental plots, DFA: Deer's Farm adjacent, HFA: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood.

	W	DF	DFA	HF	HFA
DF	**Z = 0.289** **p = 1**				
DFA	**Z = 2.74** **p < 0.05 ***	**Z = 3.07** **p < 0.05 ***			
HF	**Z = 0.18** **p = 1**	**Z = -0.15** **p = 1**	**Z = -3.17** **p < 0.05 ***		
HFA	**Z = 1.04** **p = 1**	**Z = 0.99** **p = 1**	**Z = -1.7** **p > 0.05**	**Z = 1.1** **p = 1**	
H	**Z = 0.62** **p = 1**	**Z = 0.47** **p = 1**	**Z = -2.12** **p > 0.05**	**Z = 0.58** **p = 1**	**Z = -0.42** **p = 1**

Table 9. Dunn's post-hoc test results: Z statistics and p values for multiple comparisons of total available Nitrogen Kg/ha between sites. *'s denote results were there was a significant difference. DF: Deer's Farm RHS experimental plots, HF: Howard's Field RHS experimental plots, DFA: Deer's Farm adjacent, HFA: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood.

	W	DF	DFA	HF	HFA
DF	**Z = -3.06** **p < 0.05 ***				
DFA	**Z = -3.49** **p < 0.01 ****	**Z = -1.21** **p = 1**			
HF	**Z = -2.8** **p < 0.05 ***	**Z = -0.37** **p = 1**	**Z = -1.47** **p = 1**		
HFA	**Z = -3.42** **p < 0.01 ****	**Z = 1.13** **p = 1**	**Z = -0.07** **p = 1**	**Z = -1.39** **p = 1**	
H	**Z = -3.37** **p < 0.01 ****	**Z = 1.07** **p = 1**	**Z = -0.12** **p = 1**	**Z = -1.33** **p = 1**	**Z = 0.05** **p = 1**

Table 10. Dunn's post-hoc test results: Z statistics and p values for multiple comparisons of Nitrate ($NO3^-$) mg/Kg between sites. *'s denote results were there was a significant difference. DF: Deer's Farm RHS experimental plots, HF: Howard's Field RHS experimental plots, DFA: Deer's Farm adjacent, HFA: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood.

	W	DF	DFA	HF	HFA
DF	**Z = -2.62** **p > 0.05**				
DFA	**Z = -3.75** **p < 0.01 ****	**Z = -1.98** **p > 0.05**			
HF	**Z = -2.41** **p > 0.05**	**Z = -0.30** **p = 1**	**Z = -2.19** **p > 0.05**		
HFA	**Z = -3.41** **p < 0.01 ****	**Z = 1.55** **p > 0.05**	**Z = -0.35** **p = 1**	**Z = -1.76** **p > 0.05**	
H	**Z = -4.17** **p < 0.001 *****	**Z = 2.48** **p > 0.09**	**Z = 0.41** **p = 1**	**Z = -2.69** **p > 0.05**	**Z = -0.76** **p = 1**

Appendix 3.2.

Table 1. Mean soil moisture content of each plot for each sampling occasion (percentage volumetric water content).

Site/ treatment	Plot	Oct '11		Apr '12		July '12		Oct '12		Apr '13	
		C	D	E	F	G	H	I	J	K	L
Deer's N	D5NB	8.5	8	13.8	31.0	17.6	22.1	12.6	19.1	29.2	16.0
	D3NA	7.9	10.6	22.2	28.5	19.8	8.1	8.9	21.9	25.4	18.8
	D1NB	9.1	14.2	19.2	23.3	21.8	28.3	18.4	22.3	25.0	20.7
	D2NC	11.2	10.6	19.1	26.3	19.1	22.8	18.0	22.0	27.1	10.3
	D6NC	9.5	8.3	15.1	13.9	22.9	21.3	18.7	17.0	25.5	11.3
	D4NA	9.3	7.3	23.7	25.0	11.4	18.1	15.0	20.5	21.6	18.3
Deer's Z	D1ZB	7	17.8	16.7	26.9	14.8	16.0	19.9	21.4	33.8	23.6
	D3ZA	9.3	11	13.7	25.8	21.4	23.3	22.2	16.2	26.0	15.0
	D5ZB	7.3	9.6	18.5	23.9	14.6	13.1	18.8	20.7	20.5	19.1
	D2ZC	13.5	5.6	19	14.9	21.4	26.1	5.2	22.9	30.6	11.5
	D4ZA	9.6	9.7	11.6	32.4	19.9	16.2	19.0	24.3	16.1	16.3
	D6ZC	6.9	13.2	14.1	27.0	15.5	16.4	16.8	23.1	24.6	17.3
Deer's E	D1EB	10.5	9.4	14.7	30.1	17.9	20.0	21.0	19.4	22.1	15.7
	D3EA	9.3	8.5	10.3	25.6	16.1	14.2	20.3	8.5	34.9	27.3
	D5EB	11.7	7.2	17.8	22.6	20.0	18.5	12.1	18.0	21.1	13.4
	D6EC	10.9	11.3	9.3	10.0	15.8	10.4	13.3	6.9	30.0	17.0
	D4EA	9.2	8.9	8	22.7	10.9	15.3	16.7	25.1	23.8	19.0
	D2EC	8.7	7.8	10.9	13.2	14.1	12.9	19.7	18.8	27.4	15.5
Howard's N	H1NA	10.2	9.7	22.4	24.8	22.6	13.8	26.0	24.8	19.6	13.4
	H5NB	11	15.6	19.3	21.8	26.7	14.5	18.1	17.4	23.7	15.0
	H3NC	9.9	13.7	25.1	22.2	23.7	20.6	22.9	22.0	19.2	19.7
	H2NB	6.7	8.8	19.5	28.8	23.7	16.5	13.7	21.2	15.9	21.5
	H6NA	7.9	7.3	9.2	27.6	23.6	14.3	16.7	20.6	19.1	15.2
	H4NC	9.2	4.9	22.6	29.3	23.4	12.7	9.1	20.8	17.2	13.5
Howard's Z	H5ZB	7.7	11	24.7	30.9	25.8	11.9	20.1	13.6	18.9	18.2
	H3ZC	8.9	12.3	18.8	24.8	12.0	15.8	22.8	17.8	18.7	16.4
	H1ZA	9.9	9	26.1	22.1	25.9	16.0	7.7	23.7	22.0	15.9
	H2ZB	11.6	8	18.8	27.0	26.7	14.6	17.8	8.2	19.6	9.9
	H4ZC	12.2	6	22.7	28.0	21.9	6.8	19.2	20.0	18.6	14.0
	H6ZA	13.5	11.4	9.5	27.3	22.0	12.0	12.9	21.0	17.6	9.7
Howard's E	H3EC	13	12.2	20.1	29.9	21.5	22.6	7.5	20.2	19.8	13.4
	H1EA	12.5	10.5	21	27.1	25.1	14.5	11.5	13.0	22.1	20.1
	H5EB	13.4	19.7	18.9	25.6	24.7	19.9	21.5	16.3	17.9	14.1
	H6EA	13.2	17.6	22.5	26.1	25.1	18.4	19.5	18.8	17.2	18.6
	H4EC	16.8	15.3	23.8	25.2	24.3	25.9	21.8	21.9	20.0	10.8
	H2EB	8.2	7.3	16	28.4	25.9	11.2	17.2	23.4	21.1	20.4
Deer's A	DA1	8.5	7.6	16.8	35.7*	29.8	14.3*	29.3	27.9*	26.7*	18.5
	DA2	13.8	8.3	15.2*	32.9	26.1	9.8	14.9	35.0*	26.9	26.3*
	DA3	7.8	6.5	17.7	45.1*	26.2	9.7*	14.3	23.2*	22.3	22.2*
	DA4	10.1	7.2	15.4*	34.3	25.0	9.8*	14.1	29.0*	23.4*	11.6
	DA5	7.6	6.8	12.1	30.0*	28.2*	4.0	19.3*	22.3	22.5*	16.6
	DA6	7.3	6.5	13.7*	28.7	29.5*	14.5	19.5	22.5	27.1	16.5*

Howard's A	HA1	21.1	18.9	18.7	29.8*	31.2	14.6*	24.1*	30.5	32.9	25.9
	HA2	13.9	19.2	18.5	32.7*	30.7*	14.2	20.4	24.1*	23.6	15.4
	HA3	17.3	22	20.8*	38.7	31.3	11.3*	22.2*	26.7	24.1*	11.9
	HA4	15.1	9.1	20.1*	46.3	30.7	7.9*	19.9	24.8*	20.9*	15.2
	HA5	11.1	8.3	19.9*	36.5	32.7*	15.3	25.4	26.2*	23.7	12.6
	HA6	9.9	9.4	19.9	37.1*	33.9*	13.1	27.5*	26.8	23.7	14.4
Wisley Common	H1	25.5	24.1	30	47.8	34.6	17.3	39.6	25.4	39.9	26.1
	H2	20.8	17.7	33.4	36.9	39.4	18.0	32.6	36.2	37.4	28.0
	H3	12.3	14.7	24.9	41.4	37.0	17.8	31.1	23.5	37.9	24.8
	H4	9	29.3	32	41.8	22.5	12.9	23.3	35.3	38.9	25.0
	H5	10.6	24	17	25.3	46.8	13.7	25.2	28.6	19.6	15.2
	H6	9.5	16.7	41.9	40.5	27.8	8.7	19.4	28.5	36.0	21.6
Buxton Wood	W1	23.1	17.2	26.4	29.0	37.4	32.7	31.6	33.8	27.8	30.0
	W2	12.4	20.3	35	30.4	40.3	35.9	34.0	32.9	35.9	35.7
	W3	10.8	12	30.8	27.8	20.2	23.0	36.5	25.0	40.0	32.4
	W4	11.5	12.3	35.9	33.5	29.5	28.4	24.8	17.9	28.2	20.7
	W5	8.1	6.1	28.4	18.4	30.5	22.1	8.5	13.0	27.3	14.2
	W6	8.7	24.2	28.2	43.6	24.6	22.5	32.3	32.7	30.8	29.2

* = where soil fauna extracted from cores were not sorted or counted.

Table 2. Deer's Farm weather station data: rainfall (mm), for the months that matched with the sampling occasions.

Day of the Month	July '11	Oct '11	Apr '12	July '12	Oct '12	Apr '13
1	0	0	0	0.6	4.6	0
2	0	0	0	2.4	1.2	0
3	0	0	0.4	1.6	1.8	0
4	0	0	0.2	5.2	0	0.2
5	5.6	0	0	0.4	14.8	0
6	0.2	1.4	0	3.6	11.4	0
7	5	0	0	5	0	0
8	1.6	0	1	6	9.2	0
9	0	0.4	5.2	0	0.2	2
10	0	0	0.4	0.2	0	7
11	0	0	1	5.2	4.4	2.4
12	0	0	4.6	6.4	0.6	8.4
13	0	0	0.8	2.4	0.6	3
14	0	0	1.2	8.2	0.2	0
15	0	0	0	0.2	0.6	0
16	8	0	0	1.2	0.8	0
17	2.6	0.2	1.8	2.4	12.6	0
18	5	4	7.6	1.2	0.8	4.6
19	7.4	0.8	5.6	0	7.8	0
20	0.6	0	3.4	1.4	4.6	0
21	3	0	2.6	0	2.2	0
22	6	0	4.2	0	0.4	0
23	0.8	0	2.4	0	0.2	0
24	0	2	2.2	0	0	0.2
25	0	0.8	21	0	0	0

26	0	12.2	3	0	0.4	2.4
27	0	3	3.6	0	0.8	1
28	0	0	10.4	0	1.4	0
29	0	0	14	9.4	1.2	0
30	0	0	0	0	0.2	0
31	0	0.2	NA	1.8	0.4	NA
Total rainfall	45.8	25	96.6	64.8	83.4	31.2

Table 3. RHS experimental plot % vegetation cover, dates closest to soil core sampling.

	July '11		**Oct '11**		**Apr '12**	**July '12**		**Oct '12**	**Apr '13**	
Plot	Jun '11	Aug '11	Sep '11	Nov '11	Apr '12	Jun '12	Aug '12	Oct '12	Feb '13	May '13
D5NB	0.88	0.88	0.93	0.83	0.65	0.98	0.96	0.95	0.83	0.88
D3NA	0.79	0.80	0.77	0.64	0.50	0.85	0.82	0.83	0.76	0.75
D1NB	0.73	0.80	0.73	0.74	0.50	NA	NA	0.95	0.89	0.77
D2NC	0.71	0.72	0.68	0.58	0.31	0.63	0.75	0.64	0.61	0.41
D6NC	0.66	0.58	0.50	0.42	0.39	0.65	0.78	0.55	0.49	0.39
D4NA	0.83	0.78	0.76	0.67	0.39	0.74	NA	0.86	0.86	0.69
D1ZB	0.72	0.75	0.70	0.50	0.33	NA	0.68	0.63	0.54	0.38
D3ZA	0.74	0.86	0.79	0.56	0.56	0.80	0.84	0.72	0.55	0.66
D5ZB	0.64	0.68	0.65	0.59	0.37	0.63	0.64	0.47	0.37	0.33
D2ZC	0.81	0.89	0.88	0.76	0.43	0.55	0.70	0.54	0.41	0.33
D4ZA	0.85	0.77	0.71	0.61	0.50	0.74	0.76	0.77	0.63	0.60
D6ZC	0.69	0.76	0.75	0.66	0.50	0.58	0.66	0.48	0.44	0.40
D1EB	0.64	0.68	0.74	0.70	0.56	0.73	0.76	0.68	0.72	0.49
D3EA	0.41	0.64	0.69	0.56	0.44	0.58	0.82	0.78	0.62	0.59
D5EB	0.38	0.48	0.56	0.54	0.34	0.50	0.50	0.50	0.41	0.40
D6EC	0.66	0.67	0.80	0.72	0.56	0.73	0.77	0.74	0.75	0.60
D4EA	0.47	0.62	0.66	0.60	0.48	0.65	0.81	0.77	0.69	0.48
D2EC	0.73	0.82	0.84	0.81	0.68	0.77	0.80	0.75	0.71	0.60
H1NA	0.96	0.99	1.00	1.00	0.36	0.92	1.00	0.93	0.79	0.96
H5NB	0.99	1.00	1.00	0.96	0.65	0.98	0.99	0.94	0.90	0.96
H3NC	0.95	0.92	0.96	0.91	0.43	0.88	1.00	0.98	0.83	0.82
H2NB	0.97	0.96	0.97	0.97	0.59	1.00	1.00	0.97	0.89	0.98
H6NA	0.89	0.87	0.92	0.83	0.55	0.96	0.98	0.93	0.80	0.83
H4NC	0.74	0.83	0.91	0.71	0.30	0.85	1.00	0.87	0.63	0.73
H5ZB	0.93	0.98	0.93	0.71	0.40	0.85	0.96	0.88	0.65	0.64
H3ZC	0.94	0.90	0.81	0.70	0.41	0.74	0.98	0.81	0.66	0.51
H1ZA	0.69	0.67	0.69	0.67	0.53	0.80	0.93	0.81	0.64	0.64
H2ZB	0.84	0.80	0.82	0.60	0.38	0.72	0.95	0.85	0.73	0.60
H4ZC	0.93	0.93	0.85	0.60	0.38	0.75	0.96	0.85	0.47	0.65
H6ZA	0.69	0.64	0.68	0.66	0.45	0.72	0.70	0.54	0.64	0.54
H3EC	0.85	0.81	0.87	0.87	0.67	0.86	0.94	0.92	0.92	0.56
H1EA	0.44	0.67	0.76	0.70	0.40	0.59	0.78	0.82	0.74	0.50
H5EB	0.59	0.77	0.87	0.70	0.51	0.83	0.80	0.81	0.67	0.42
H6EA	0.54	0.80	0.83	0.73	0.46	0.80	0.96	0.90	0.95	0.62
H4EC	0.71	0.88	0.90	0.82	0.48	0.81	0.91	0.89	0.77	0.50
H2EB	0.44	0.52	0.51	0.49	0.40	0.47	0.59	0.67	0.63	0.40

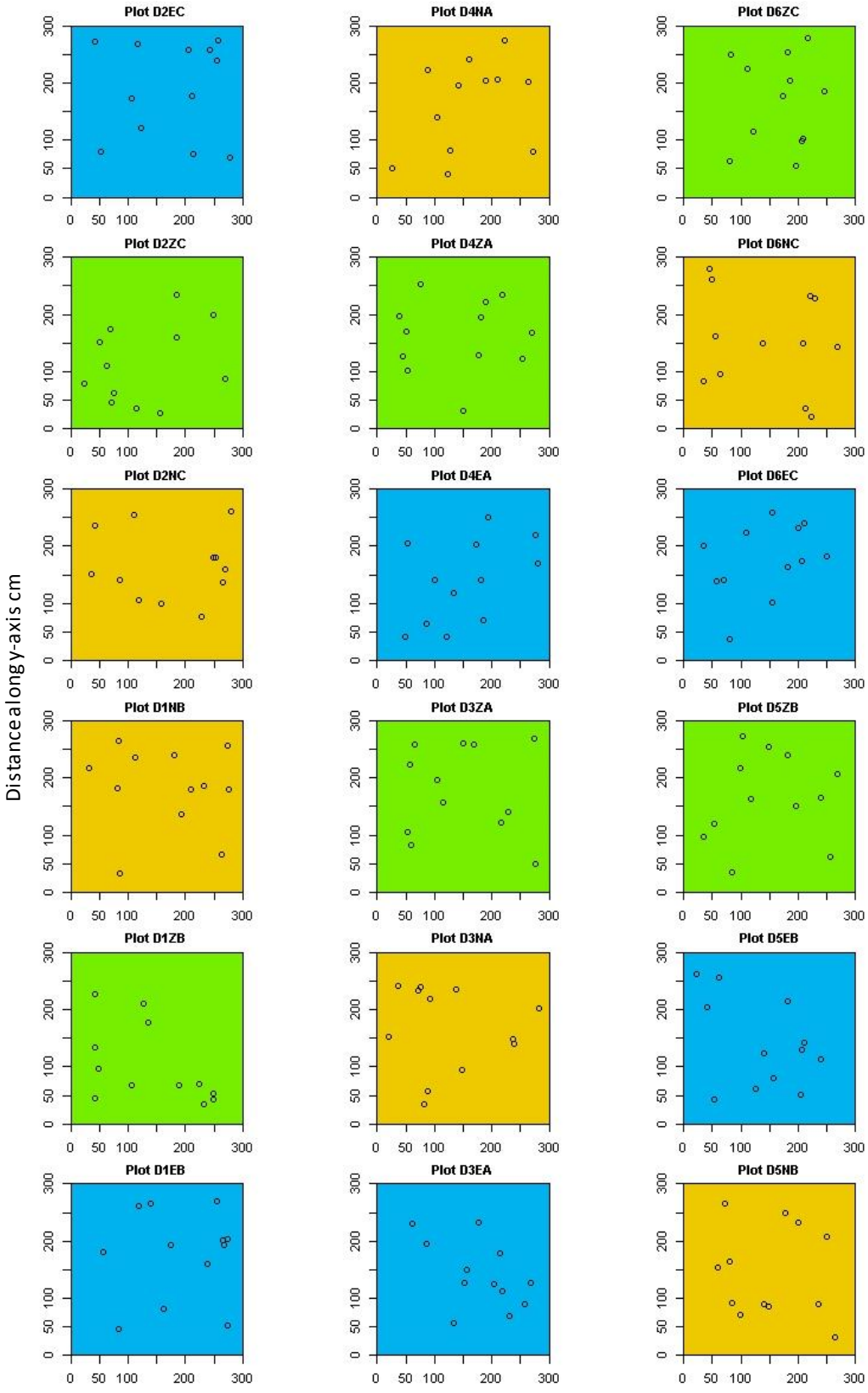

Figure 1. Deer's Farm RHS experimental plots: position of random soil core sampling, yellow = Native plots, green = Near native plots and blue = Exotic plots.

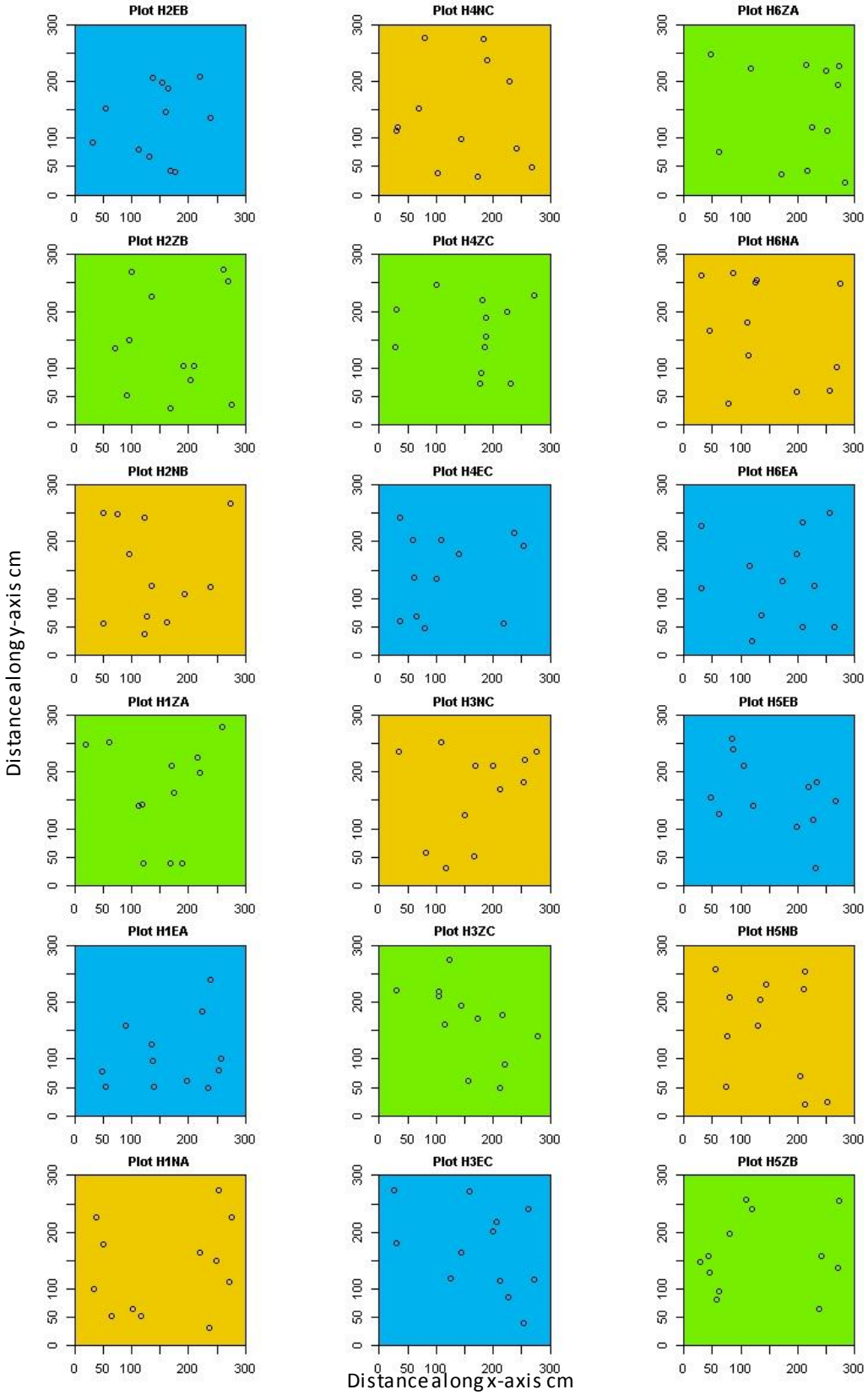

Figure 2. Howard's Field RHS experimental plots: position of random soil core sampling, yellow = Native plots, green = Near native plots and blue = Exotic plots.

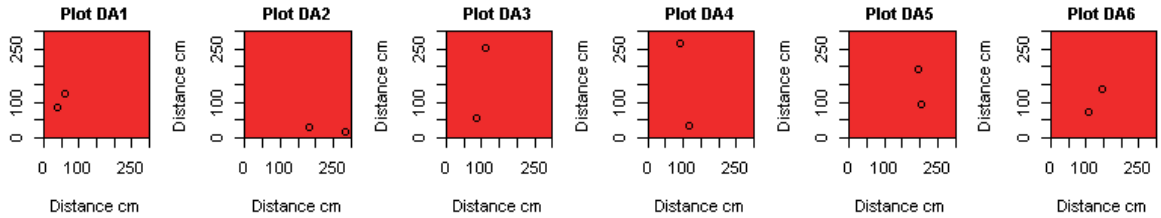

Figure 3. Deer's Farm adjacent plots: position of July '11 soil cores.

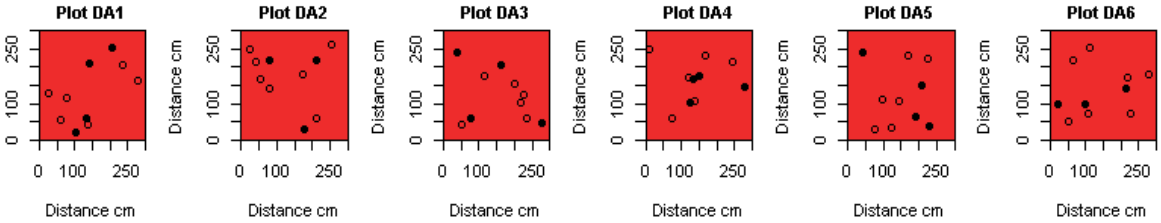

Figure 4. Deer's Farm adjacent plots: position of soil cores. Empty circles indicate where samples were processed, filled circles indicate sample for which the soil fauna were not identified.

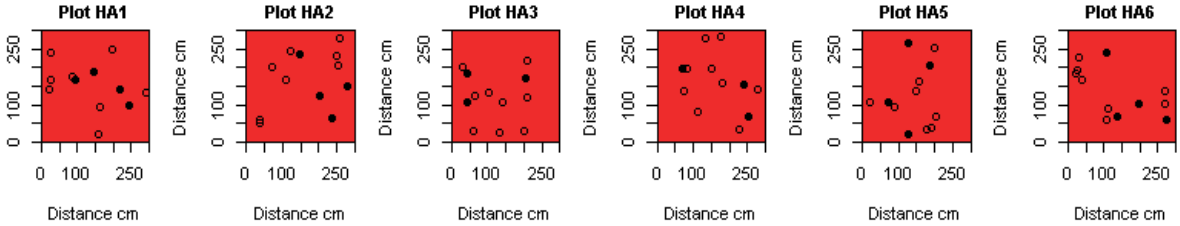

Figure 5. Howard's Field adjacent plots: position of soil cores. Empty circles indicate where samples were processed, filled circles indicate sample for which the soil fauna were not identified.

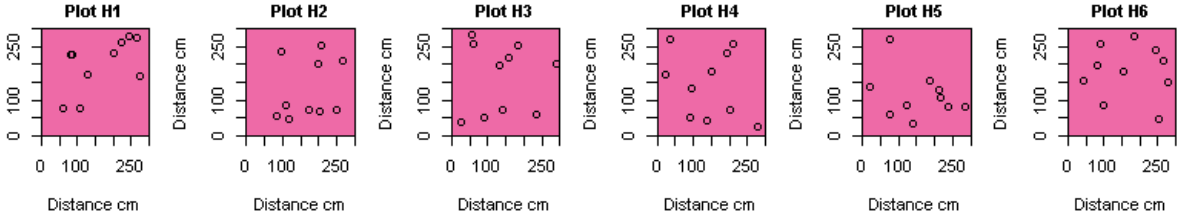

Figure 6. Wisley Common plots: position of soil cores.

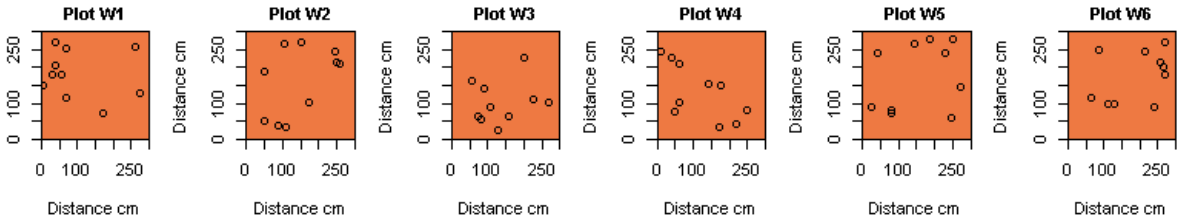

Figure 7. Buxton Wood plots: position of soil cores.

Appendix 3.4.1.

Table 1. Total abundances for the Diplopoda, found under each site/treatment. N: Native, Z: Near native, E: Exotic, A: adjacent site, H: Wisley Common, W: Buxton Wood. As the adjacent sampling site for Deer's Farm was different between July'11 and other sampling occasions, the Deer's Farm adjacent July '11 totals have been given in brackets after the overall total also including the Deer's Farm adjacent July '11 samples.

	Deer's Farm				Howard's Field					
Diplopoda	**N**	**Z**	**E**	**A**	**N**	**Z**	**E**	**A**	**H**	**W**
Brachyiulus pusilus	2	0	0	0	1	1	3	1	0	0
Cylindriolus punctatus	0	0	0	0	0	0	0	0	0	1
***Cylindriolus* sp.**	8	1	3	0	3	2	3	0	0	2
***Julida* sp.**	41	9	14	3 (2)	14	14	7	6	1	7
Ommatoiulus sabulosus	0	0	0	0	0	0	1	0	0	0
Proteroiulus fuscus	0	0	0	0	0	0	0	0	0	1
Macrosternodesmus palicola	0	1	0	0	0	0	3	0	0	0
Polydesmida	0	0	0	0	3	1	4	0	3	0
Anthogona brittanica	0	0	0	0	2	0	2	0	0	0
Anthogonidae	0	0	0	0	0	0	0	0	0	1
Polyxenus lagurus	0	0	0	0	0	0	0	0	2	0

Table 2. Total abundances for the adult Coleoptera, found under each site/treatment. N: Native, Z: Near native, E: Exotic, A: adjacent site, H: Wisley Common, W: Buxton Wood. As the adjacent sampling site for Deer's Farm was different between July '11 and other sampling occasions, the Deer's Farm adjacent July '11 totals have been given in brackets after the overall total also including the Deer's Farm adjacent July '11 samples.

Coleoptera		Deer's Farm				Howard's Field					
Family	**Identification level**	**N**	**Z**	**E**	**A**	**N**	**Z**	**E**	**A**	**H**	**W**
Carabidae	*Amara* sp.	0	0	0	3	0	0	0	0	1	0
	Harpalus affinis	1	0	0	0	0	0	0	0	0	0
	Harpalus sp.	2	3	0	0	0	0	0	0	1	1
	Syntomus foveatus	0	0	1	0	0	1	0	1	0	0
	Carabidae	0	0	0	1	0	0	0	0	0	0
Curculionidae	Cryptorhynchinae sp. A	0	0	1	1	0	0	0	0	2	0
	Cryptorhynchinae sp. B	0	1	1	4	1	1	0	3	0	0
	Trachyphloeus sp.	5	2	0	7	0	1	0	5	1	0
Chrysomelidae	Chryptocephalinae	0	0	0	0	0	0	0	0	1	0
Staphylinidae	Aleocharinae	4	3	0	20 (3)	2	3	1	11	0	1
	Anotylus sp.	0	0	0	0	1	0	0	0	0	0
	Xantholinus linearis	0	2	1	1 (1)	4	2	0	1	0	0
	Staphylinidae	1	1	0	4 (2)	3	4	3	7	1	3
Ptilidae	Ptilidae	0	0	0	2 (2)	2	0	0	1	0	1
Histeridae	Histeridae	2	0	0	0	1	0	0	7	0	0
Lathridiidae	Lathridiidae	0	1	1	0	0	0	0	0	0	0
Elateridae	Elateridae	0	0	0	0	0	0	0	0	0	4
Throscidae	*Trixagus dermestiodes*	0	0	0	0	0	2	0	0	0	0
	Coleoptera	0	0	0	1 (1)	4	0	1	0	3	1

Appendix 3.4.2.

Table 1. Total abundance of Collembola under each site/treatment for each sampling occasion.

		Total Collembola abundance each sampling occasion					
Site	**Treatment**	**July '11**	**Oct '11**	**Apr '12**	**Jul '12**	**Oct '12**	**Apr '13**
Deer's Farm	**Native**	42	287	180	287	117	251
	Near Native	4	171	111	171	94	213
	Exotic	27	54	123	54	113	219
	Adjacent	338	330	346	330	240	102
Howard's Field	**Native**	49	345	386	345	126	264
	Near Native	82	382	79	382	325	229
	Exotic	49	120	86	120	57	129
	Adjacent	333	436	231	436	337	364
Wisley Common		NA	454	88	454	289	254
Buxton Wood		NA	265	162	265	114	398

Table 2. List of all the Collembola species found and their authorities.

Taxa (Genus/Genus and species)	Species code	Authority
Cryptopygus thermophilus	CRthe	(Axelson, 1900)
Desoria tigrina	DOtig	Nicolet, 1842
Folsomia	FO	Willem, 1902
Folsomia candida	FOcan	Willem, 1902
Folsomia quadrioculata	FOquo	(Tullberg, 1871)
Folsomia manolachei	FOman	Bagnall, 1939
Folsomia spinosa	FOspi	Kseneman, 1936
Isotoma	IS	Bourlet, 1839
Isotoma anglicana	ISang	Lubbock, 1862
Isotoma viridis	ISvir	Bourlet, 1839
Isotomiella minor	IMmin	(Schäffer, 1896)
Isotomodes productus	ITpro	(Axelson, 1906)
Isotomurus palustris	IRpal	Müller, 1776
Isotomurus prasinus	IRpra	Reuter, 1891
Mucrosomia garretti	MUgar	(Bagnall, 1939)
Parisotoma notabilis	POnot	Schäffer, 1896
Proisotoma minuta	PImit	(Tullberg, 1871)
Proisotoma minima	PImin	(Absolon, 1901)
Pseudisotoma sensibilis	PEsen	(Tullberg, 1876)
Tomocerus	TO	Nicolet, 1841
Cyphoderus albinus	CYalb	Nicolet, 1842
Entomobrya	EN	Rondani, 1861
Entomobrya intermedia	ENint	Brook, 1883
Entomobrya marginata	ENmar	(Tullberg, 1871)
Entomobrya multifasciata	ENmul	(Tullberg, 1871)
Entomobrya nicoleti	ENnic	(Lubbock, 1867)
Entomobrya nivalis	ENniv	(Linnaeus, 1758)

Heteromurus major	HTmaj	(Moniez, 1889)
Lepidocyrtus	LE	Bourlet, 1839
Lepidocyrtus cyaneus	LEcya	Tullberg, 1871
Lepidocyrtus curvicolis	LEcur	Bourlet, 1839
Lepidocyrtus lanuginosus	LElan	(Gmelin, 1788)
Lepidocyrtus lignorum	LElig	(Fabricius, 1775)
Orchesella cincta	ORcin	(Linnaeus, 1758)
Willemia intermedia	WLint	Mills, 1934
Willemia anopthalma	WLano	Börner, 1901
Willemia denisi	WLden	Mills, 1932
Schoettella ununguiculata	SHung	(Tullberg, 1869)
Xenylla boerneri	XLboe	Axelson, 1905
Ceratophysella denticulata	CEden	(Bagnall, 1941)
Brachystomella parvula	BRpar	(Schäffer, 1896)
Friesea	FR	Dalle Torre 1895
Friesea claviseta	FRcla	Axelson, 1900
Friesea mirabilis	FRmir	(Tullberg, 1871)
Friesea truncata	FRtru	Cassagnau, 1958
Micranurida forsslundi	MIfor	Gisin, 1949
Micranurida pygmaea	MIpyg	Börner, 1901
Neanura muscorum	NNmus	(Templeton, 1835)
Deuteraphorura inermis	DUine	(Tullberg, 1871)
Onychiurus ambulans	ONamb	(Linnaeus, 1758)
Protaphorura	PR	Absolon, 1901
Protaphorura armata	PRarm	(Tullberg, 1869)
Supraphorura furcifera	SRfur	(Börner, 1901)
Paratullbergia callipygos	PTcal	(Börner, 1902)
Mesaphorura	MS	Börner, 1901
Mesaphorura macrochaeta	MSmac	Rusek, 1976
Sminthurinus	SN	Börner, 1901
Sminthurinus aureus	SNaur	(Lubbock, 1862)
Sminthurinus elegans	SNele	(Fitch, 1863)
Sminthurinus reticulatus	SNret	Cassagnau, 1964
Katianna species 4	KA '4'	NA
Katianna schoetti	KAsch	Womersley, 1933
Lipothrix lubbocki	LIlub	(Tullberg, 1872)
Sminthurus nigromaculatus	SMnig	(Tullberg, 1872)
Sminthurides	SD	Börner, 1900
Sminthurides malmgreni	SDmal	(Tulberg, 1876)
Sminthurides parvulus	SDpar	(Krausbauer, 1898)
Sminthurides schoetti	SDsch	Axelson, 1903
Sphaeridia pumilis	SPpum	(Krausbauer, 1898)
Bourletiella arvalis	BOarv	(Fitch, 1863)
Bourletiella hortensis	BOhor	(Fitch, 1863)
Deuterosminthurus bicinctus	DEbic	(Koch, 1840)
Deuterosminthurus pallipes	DEpal	(Bourlet, 1843)
Deuterosminthurus sulphureus	DEsul	(Koch, 1840)
Heterosminthurus bilineatus	HSbil	(Bourlet, 1842)

Dicyrtoma fusca	DIfus	(Lubbock, 1873)
Dicyrtomina saundersi	DMsau	(Lubbock, 1862)
Megalothorax minimus	MGmin	Willem, 1900

Table 3. Total abundances for Collembola species found under each site/treatment. N = Native, Z = Near native, E = Exotic, A = Adjacent site, H = Wisley Common, W = Buxton Wood. As the adjacent sampling site for Deer's Farm was different between July'11 and other sampling occasions the Deer's Farm adjacent July'11 totals have been given in brackets after the overall total also including the Deer's Farm adjacent July '11 samples.

	Deer's Farm				Howard's Field					
Taxa	**N**	**Z**	**E**	**A**	**N**	**Z**	**E**	**A**	**H**	**W**
CRthe	2	0	0	284 (3)	1	1	1	1073	0	0
DOtig	0	1	7	0	1	7	4	4	0	0
FOcan	0	0	0	0	0	0	0	0	3	0
FOquo group	1	25	0	43 (43)	24	34	2	10	829	441
FOspi	0	0	0	0	0	1	2	0	0	0
ISang & ISvir	15	17	24	268 (8)	26	12	9	266	4	1
IMmin	0	0	0	0	1	1	1	0	27	38
ITpro	10	27	0	147 (0)	3	2	1	183	0	0
IRpal	0	0	0	0	0	0	0	0	30	0
IRpra	0	0	0	0	0	0	1	0	1	0
MUgar	0	0	1	1 (1)	3	3	0	0	0	0
POnot	559	351	306	112 (36)	645	701	295	34	96	430
PImit	0	0	0	0	0	1	0	7	0	0
PImin	0	0	0	0	0	0	0	0	0	1
PEsen	0	0	0	0	1	0	0	0	260	1
TO	0	0	0	0	0	0	0	0	5	0
CYalb	0	0	0	0	0	2	0	7	0	0
ENint	0	0	1	0	0	0	0	0	0	0
ENmar	0	0	0	0	0	0	0	0	1	0
ENmul	20	9	3	3 (0)	11	15	2	2	19	0
ENnic	2	1	0	1 (1)	3	0	0	0	16	0
Enniv	0	0	0	0	0	0	0	0	1	0
HTmaj	28	15	2	18 (0)	19	14	3	17	0	0
LEcya	2	2	1	32 (0)	1	0	0	1	6	0
LEcur	0	0	0	0	0	0	0	1	1	1
LElan	7	3	1	80 (71)	0	1	0	0	132	28
LElig	0	0	0	8 (8)	0	0	0	0	5	26
ORcin	0	0	0	2 (2)	0	0	0	0	0	1
WLint	0	0	0	0	0	203	0	0	0	0
WLano	0	3	0	0	0	0	0	0	1	0
WLden	0	0	0	0	0	0	0	0	1	0
SHung	0	0	0	0	0	0	0	0	20	0
XLboe	1	0	0	0	0	0	0	1	0	0
CEden	0	0	0	0	1	0	0	0	1	0

BRpar	0	1	1	33 (0)	0	0	0	78	0	0
FR	17	8	7	47 (37)	2	1	9	64	30	131
MIfor	0	0	0	0	0	0	0	0	5	9
MIpyg	0	0	0	0	0	0	0	0	11	17
NNmus	0	0	3	1 (1)	4	8	2	0	1	2
DUine	0	0	1	0	0	0	0	0	0	1
ONamb	0	0	0	0	0	0	0	0	0	0
PR	3	5	26	0	1	3	3	38	0	44
SRfur	0	0	0	0	0	0	0	0	0	1
PTcal	0	0	1	0	1	3	0	0	2	2
MS	53	45	48	190 (125)	25	29	15	106	54	88
SNaur	0	2	0	2 (1)	0	0	2	10	12	8
SNele	4	3	1	9 (0)	12	0	4	58	2	0
SNret	0	0	5	0	0	0	0	0	0	0
KA'4'	0	0	0	0	0	0	3	0	0	0
KAsch	0	0	0	0	0	1	4	0	0	0
LIlub	0	0	0	0	0	0	0	0	5	0
SMnig	0	0	0	0	0	0	0	0	2	0
SDmal	1	0	2	0	0	0	0	0	0	0
SDpar	0	0	0	0	0	0	0	0	1	0
SDsch	0	1	0	0	0	0	4	0	2	0
SPpum	4	3	3	163 (0)	4	4	1	228	10	0
BOarv	0	0	0	10 (0)	2	0	5	17	0	0
BOhor	0	0	0	0	0	1	0	0	0	0
DEbic	0	0	1	4 (0)	0	0	0	1	0	0
DEpal	19	2	0	12 (0)	5	9	11	31	0	0
DEsul	0	0	0	0	0	0	0	1	0	0
HSbil	0	0	0	0	0	0	0	0	7	0
DIfus	0	0	0	0	3	1	0	0	4	2
DMsau	0	0	0	0	0	0	0	0	2	2
MGmin	144	88	125	1 (1)	371	65	78	0	44	168
SD mangled *	0	0	0	0	0	0	0	0	1	0
SN mangled *	2	0	4	24 (0)	4	4	1	9	1	1
Symphypleona *	0	0	0	0	0	0	0	1	0	0
Pseudachorutinae *	0	0	2	0	0	0	0	0	0	0
Neanuroidea *	0	1	0	0	0	0	0	0	0	0
LE mangled *	2	0	0	29 (0)	0	0	0	0	15	2
EN mangled *	10	3	5	1 (0)	10	6	2	0	31	4
Entomobryidae *	1	1	0	0	0	0	0	0	5	1
Anurophorinae *	0	0	2	0	1	0	0	0	0	0
Isotomidae *	0	1	0	0	0	0	0	0	0	0
Isotominae *	0	0	1	0	0	0	0	0	0	0
Mangled *	1	0	0	0	0	0	1	1	1	0

* : mangled

Table 4. 'drop 1' significant interaction terms in RHS experimental plot Collembola abundance model including the sample collected in October '12 from H2ZB. Adjusted R^2 = 0.9927, AIC = 1739.4.

Term	d.f.	F value	p value	
Site : Treatment (interaction)	2	4.298	p = 0.015	*
Moist : Season (interaction)	2	5.011	p = 0.008	**

*: p < 0.05, **: p < 0.01

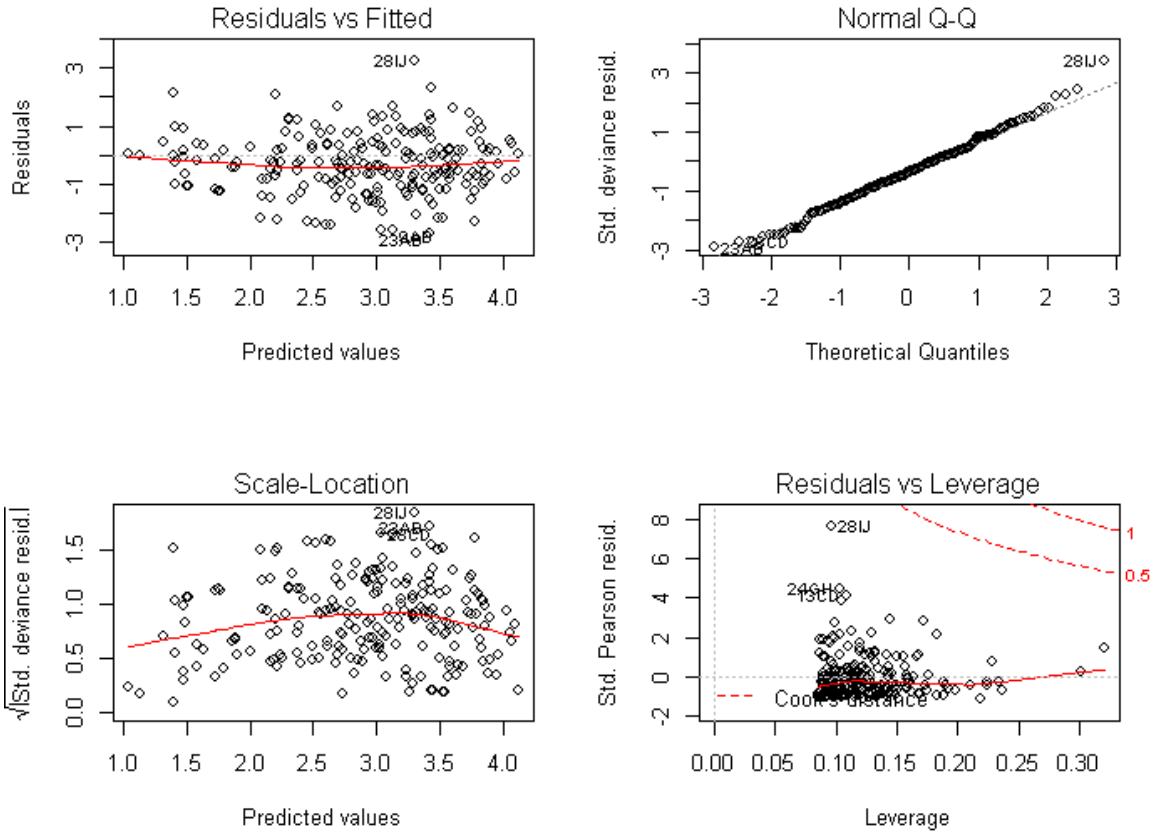

Figure 1. Plots of residuals for Collembola abundance global starting model including the sample collected in October '12, from H2ZB (point: 28IJ), prior to stepwise deletion of non-significant terms; adjusted R^2 = 0.9931, AIC = 1756.2.

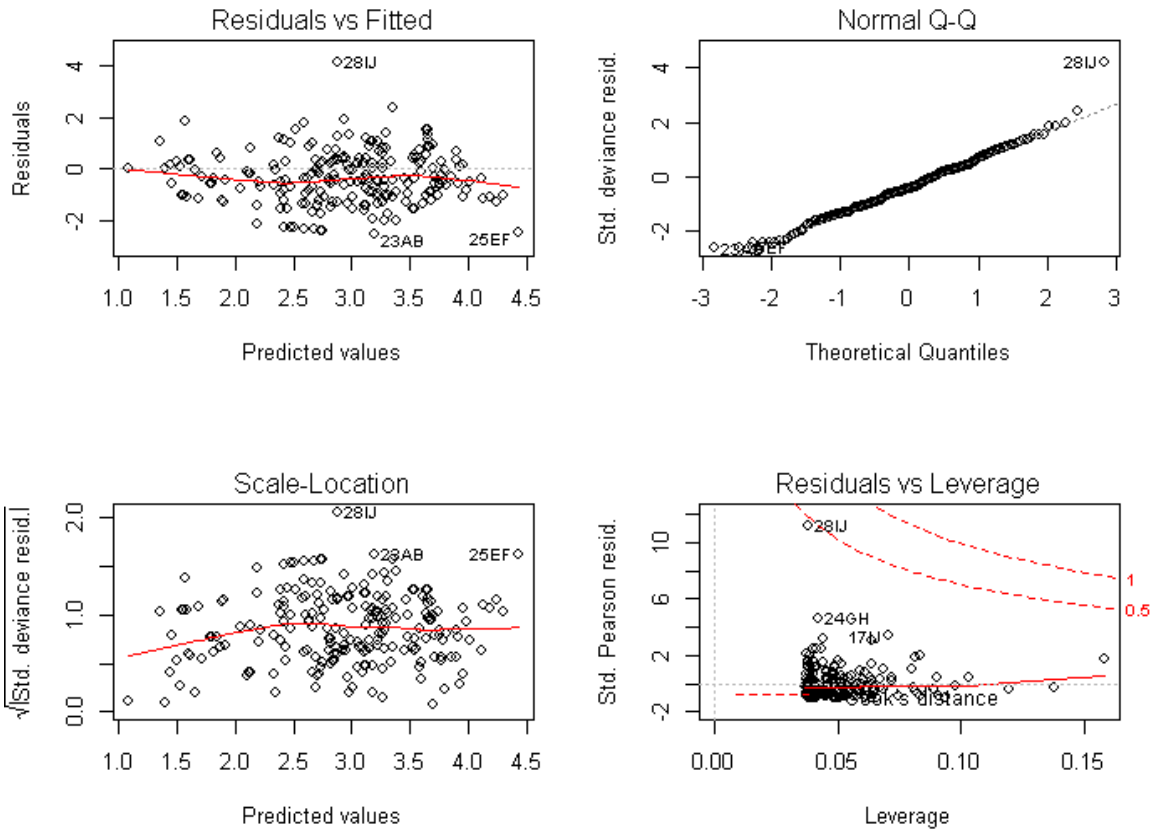

Figure 2. Plots of residuals for Collembola abundance final model including the sample collected in October '12, from H2ZB (point: 28IJ), after stepwise deletion of all non-significant terms; adjusted R^2 = 0.9927, AIC = 1739.4.

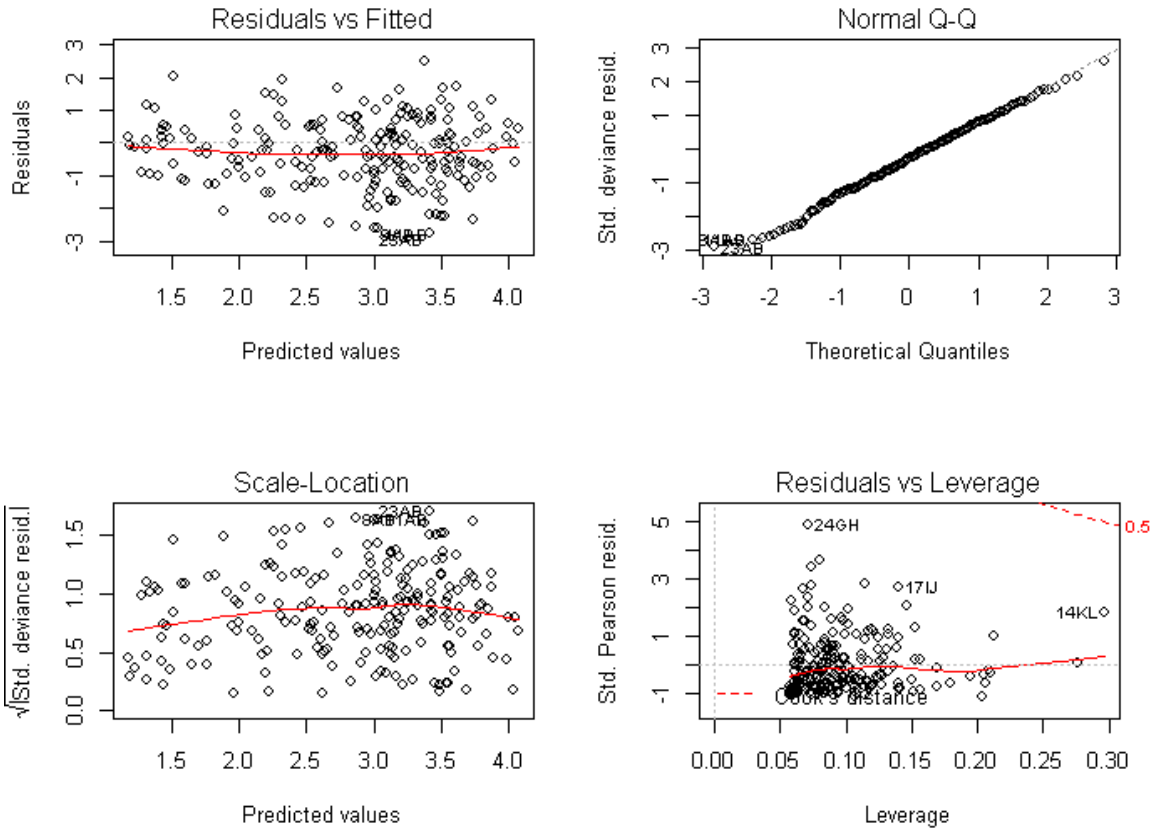

Figure 3. Plots of residuals for Collembola abundance global starting model excluding the sample collected in October '12, from H2ZB, prior to stepwise deletion of non-significant terms; adjusted R^2 = 0.9943, AIC = 1723.6.

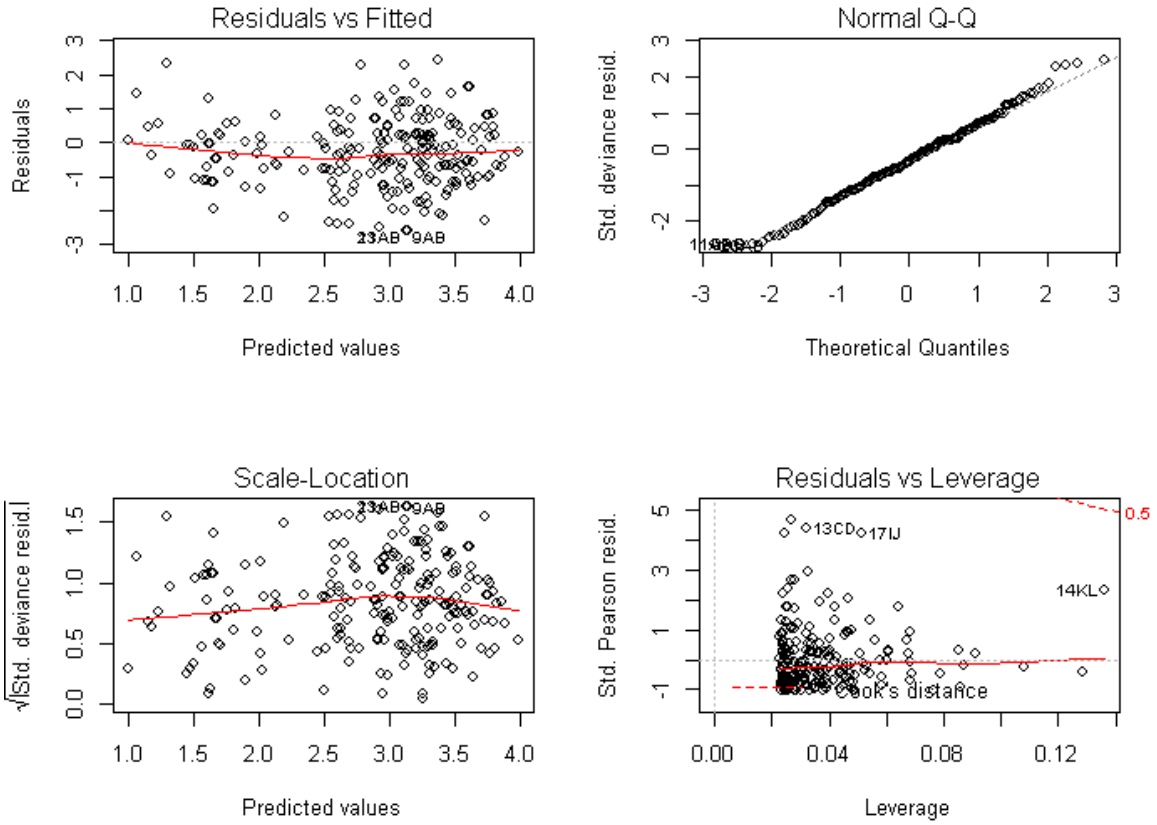

Figure 4. Plots of residuals for Collembola abundance final model excluding the sample collected in October '12, from H2ZB, after stepwise deletion of all non-significant terms; adjusted R^2 = 0.9917, AIC = 1702.4.

Appendix 3.4.3.

Table 1. Total abundance of Acari found each site/treatment for each sampling occasion.

		Total Acari abundance each sampling occasion					
Site	**Treatment**	**July '11**	**Oct '11**	**Apr '12**	**Jul '12**	**Oct '12**	**Apr '13**
Deer's Farm	**Native**	239	634	327	634	519	597
	Near native	44	499	224	499	412	606
	Exotic	117	178	360	178	286	580
	Adjacent	831	593	723	593	270	905
Howard's Field	**Native**	736	1491	446	1491	1275	815
	Near native	645	1437	349	1437	683	840
	Exotic	419	770	466	770	357	836
	Adjacent	1119	558	1276	558	886	1162
Wisley Common		NA	1853	815	1853	1242	1908
Buxton Wood		NA	276	474	276	191	620

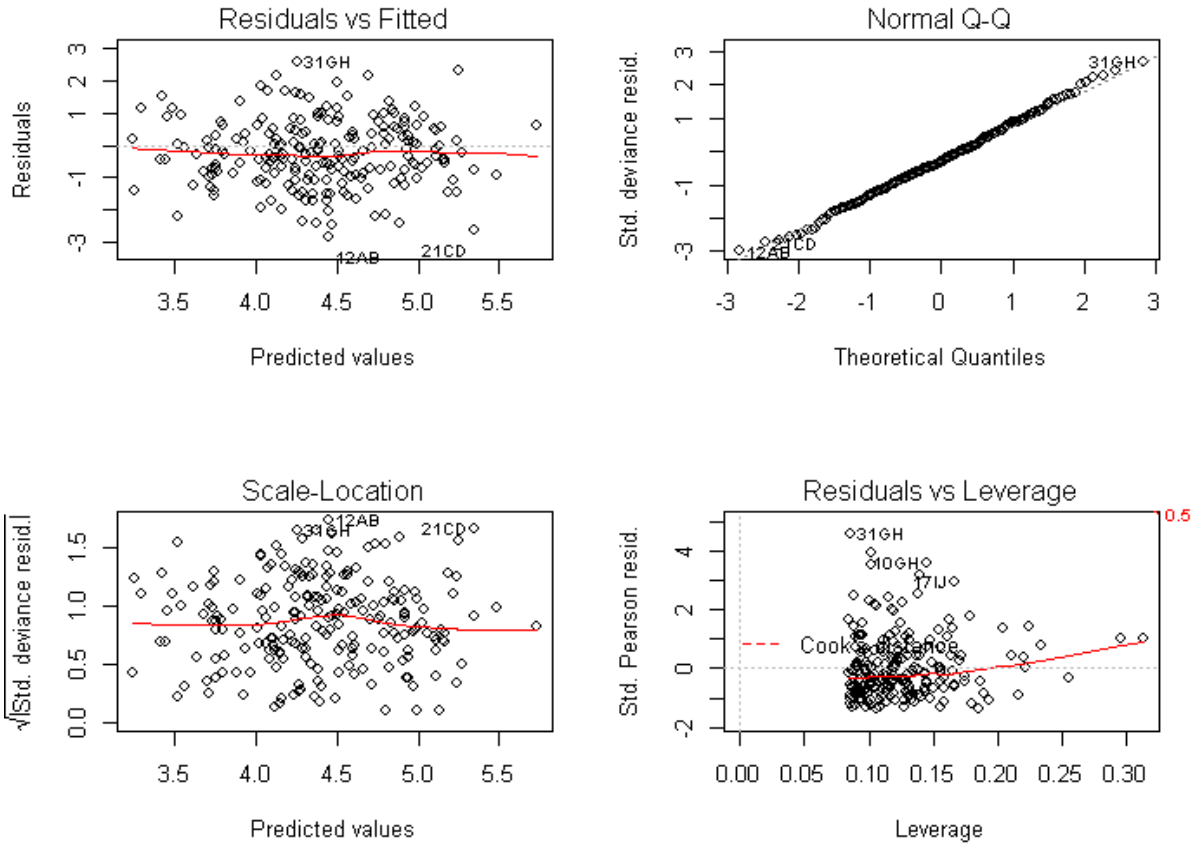

Figure 1. Plots of residuals for Acari abundance global starting model, prior to stepwise deletion of non-significant terms; adjusted R^2 = 0.9997, AIC = 2351.2.

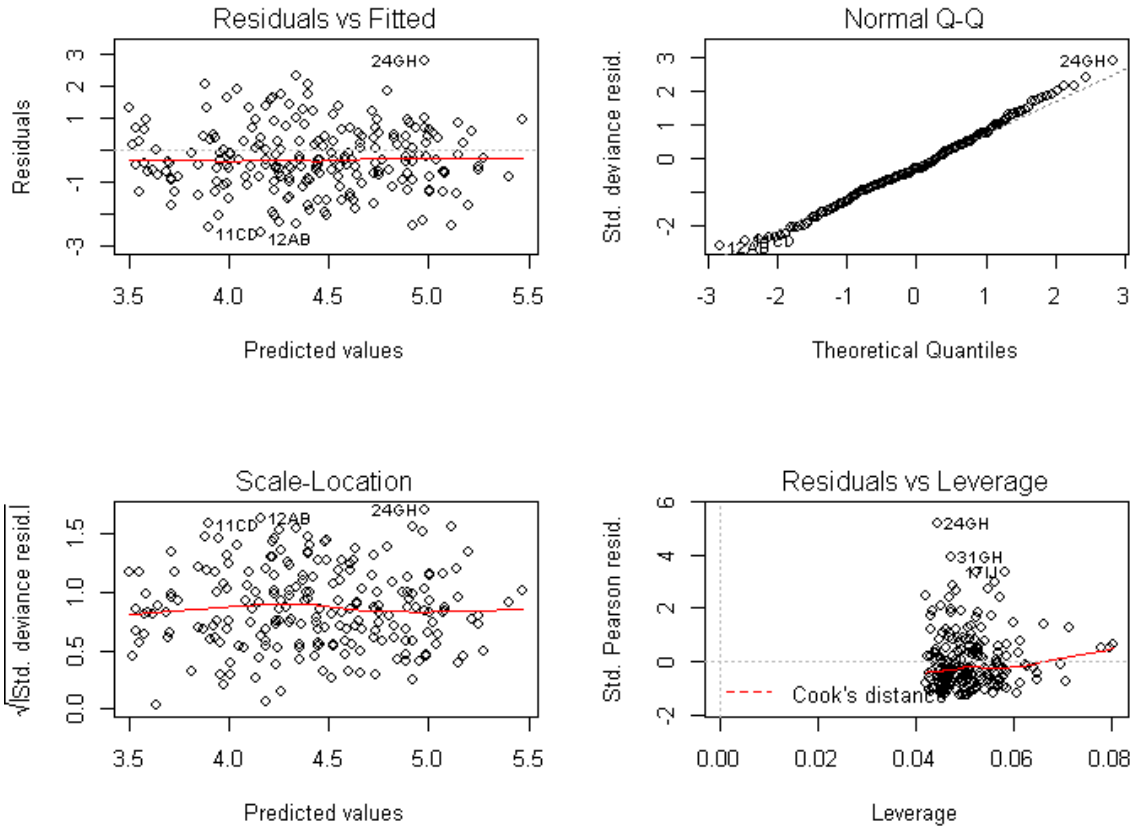

Figure 2. Plots of residuals for Acari abundance model, prior to final stepwise deletion of soil moisture; adjusted R^2 = 0.9996, AIC = 2335.1.

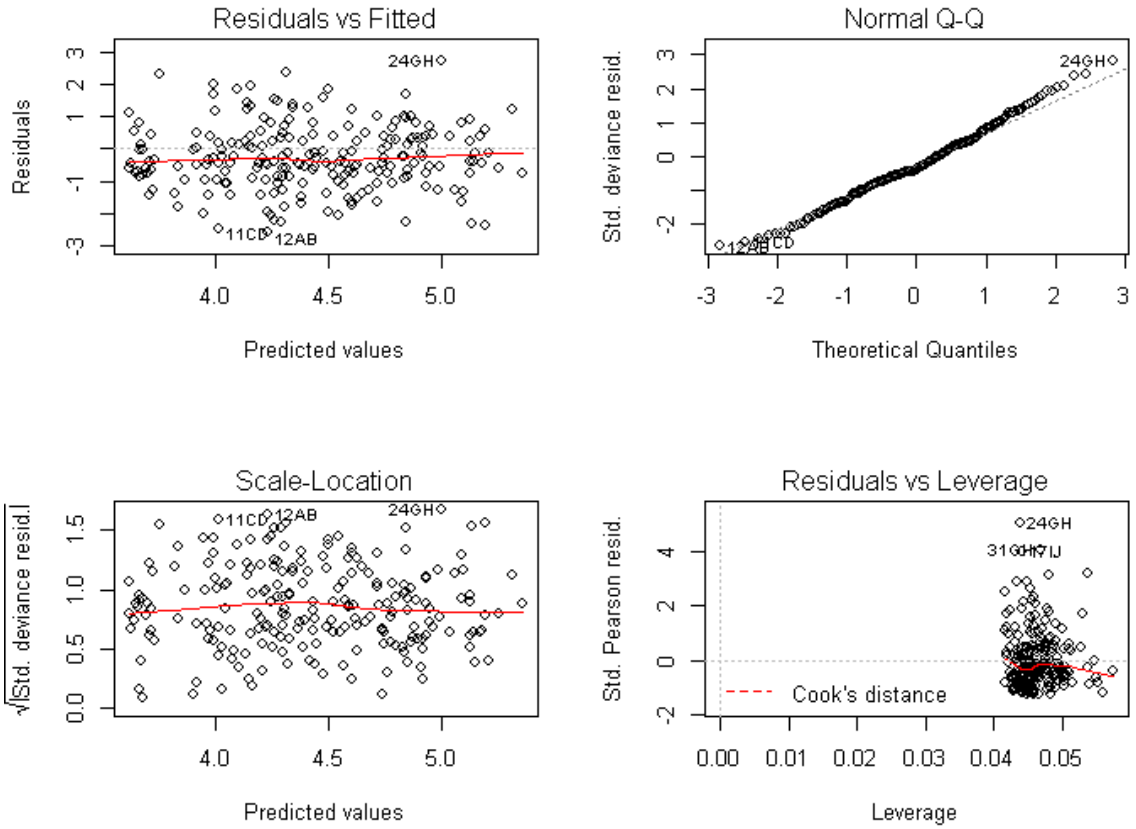

Figure 3. Plots of residuals for Acari abundance final model, after stepwise deletion of all non-significant terms; adjusted R^2 = 0.9996, AIC = 2336.

Appendix 3.4.4.

Table 1. Abundance of the Collembola species not eligible for the diversity analysis.

	Deer's Farm				Howard's Field					
Taxa	**N**	**Z**	**E**	**A**	**N**	**Z**	**E**	**A**	**H**	**W**
***Sminthurides* sp. mangled**	0	0	0	0	0	0	0	0	1	0
***Sminthurinus* sp. mangled**	2	0	4	24 (0)	4	4	1	9	1	1
Symphypleona mangled	0	0	0	0	0	0	0	1	0	0
Pseudachorutinae sp. mangled	0	0	2	0	0	0	0	0	0	0
Neanuroidea sp. mangled	0	1	0	0	0	0	0	0	0	0
***Lepidocyrtus* spp. mangled**	2	0	0	29 (0)	0	0	0	0	15	2
***Entomobrya* spp. mangled**	10	3	5	1 (0)	10	6	2	0	31	4
Entomobryidae mangled	1	1	0	0	0	0	0	0	5	1
Anurophorinae mangled	0	0	2	0	1	0	0	0	0	0
Isotomidae mangled	0	1	0	0	0	0	0	0	0	0
Isotominae mangled	0	0	1	0	0	0	0	0	0	0
Mangled	1	0	0	0	0	0	1	1	1	0

Table 2. Summary data for summer (July '11 and July '12) Collembola mean density (kg-1) per plot ± standard error for both RHS experimental plots separated by vegetation origin, with significance of between treatment effects calculated by the Kruskal-Wallis test. N = Native, Z = Near native, E = Exotic. See Appendix 3.4.2., Table 2., for interpretation of species codes.

	Deer's Farm			Howard's Field			Treatment effect
Taxa	**N**	**Z**	**E**	**N**	**Z**	**E**	
CRthe	0.21 ± 0.21	-	-	0.16 ± 0.16	0.17 ± 0.17	0.16 ± 0.16	NS
DOtig	-	-	-	-	0.17 ± 0.17	0.16 ± 0.16	NS
FOspp.	-	-	-	3.31 ± 3.09	1.38 ± 1.38	0.33 ± 0.21	NS
ISspp.	1.5 ± 1.11	1.3 ± 0.98	0.18 ± 0.18	1.92 ± 1.45	0.59 ± 0.59	1.26 ± 1.07	NS
ITpro	1.31 ± 0.68	1.13 ± 0.8	-	-	0.17 ± 0.17	0.15 ± 0.15	NS
POnot	45.56 ± 11.13	21.47 ± 6.97	6.66 ± 3.06	46.22 ± 19.59	69.43 ± 13.87	21.69 ± 7.5	*
PImin	-	-	-	-	0.17 ± 0.17	-	NS
PEsen	-	-	-	0.15 ± 0.15	-	-	NS
CYalb	-	-	-	-	0.4 ± 0.4	-	NS

ENmul	0.64 ± 0.29	0.2 ± 0.2	0.23 ± 0.23	1.57 ± 1.02	2.18 ± 0.49	0.18 ± 0.18	NS
ENnic	-	-	-	0.55 ± 0.55	-	-	NS
HTmaj	2.32 ± 0.42	1.14 ± 0.6	0.18 ± 0.18	2.66 ± 1.45	2.05 ± 1.14	0.51 ± 0.36	*
LEcya	0.22 ± 0.22	-	-	-	-	-	NS
LElan	0.88 ± 0.66	0.56 0.37	-	-	-	-	NS
WLint	-	-	-	-	0.2 ± 0.2	-	NS
BRpar	-	0.17 ± 0.17	-	-	-	-	NS
FRspp.	1.77 ± 1.32	0.34 ± 0.34	0.68 ± 0.34	-	-	0.89 ± 0.89	NS
NNmus	-	-	-	0.17 ± 0.17	0.79 ± 0.5	0.34 ± 0.22	NS
DUine	-	-	0.16 ± 0.16	-	-	-	NS
PRspp.	-	0.2 ± 0.2	2.74 ± 2.01	-	0.2 ± 0.2	0.3 ± 0.3	NS
PTcal	-	-	-	0.15 ± 0.15	-	-	NS
MSspp.	4.36 ± 2.14	2.41 ± 0.87	1.8 ± 0.86	1.49 ± 0.85	2.08 ± 0.75	0.86 ± 0.33	NS
SNaur	-	-	-	-	-	0.16 ± 0.16	NS
SNele	0.43 ± 0.43	0.2 ± 0.2	-	1.51 ± 1.32	-	-	NS
SPpum	0.86 ± 0.63	0.18 ± 0.18	-	0.7 ± 0.54	-	0.18 ± 0.18	NS
BOhor	-	-	-	-	0.2 ± 0.2	-	NS
DEpal	0.85 ± 0.63	-	-	-	1.18 0.76	1.15 ± 1.15	NS
MGmin	5.24 ± 1.98	2.76 ± 0.97	2.19 ± 2	4.47 ± 2.34	2.69 ± 1.46	0.85± 0.31	NS

-: Not recorded, NS: $p > 0.05$, *: $p < 0.05$, **: $p < 0.01$

Table 3. Summary data for autumn (October '11 and October '12) Collembola mean density (kg-1) per plot ± standard error for both RHS experimental plots separated by vegetation origin, with significance of between treatment effects calculated by the Kruskal-Wallis test. N = Native, Z = Near native, E = Exotic. See Appendix 3.4.2., Table 2., for interpretation of species codes.

	Deer's Farm			Howard's Field			Treatment effect
Taxa	**N**	**Z**	**E**	**N**	**Z**	**E**	
FOspp.	-	-	-	-	0.94 ± 0.94	-	NS
FOspi	-	-	-	-	0.19 ± 0.19	-	NS
ISspp.	-	-	0.39 ± 0.25	-	-	-	NS
IMmin	-	-	-	0.15 ± 0.15	0.17 ± 0.17	-	NS
ITpro	0.69 ± 0.69	2.67 ± 1.99	-	0.21 ± 0.21	0.16 ± 0.16	-	NS
MUgar	-	-	0.19 ± 0.19	0.42 ± 0.42	-	-	NS
POnot	12.19 ± 3.1	7.73 ± 1.99	9.9 ± 4.57	12.6 ± 3.46	18.64 ± 2.88	6.29 ± 1.77	NS
ENint	-	-	0.18 ± 0.18	-	-	-	NS
ENmul	3.29 ± 1.07	0.84 ± 0.43	0.4 ± 0.4	0.4 ± 0.26	0.32 ± 0.21	-	NS
ENnic	0.21 ± 0.21	0.19 ± 0.19	-	-	-	-	NS
HTmaj	3.24 ± 1.4	-	-	0.15 ± 0.15	-	-	**
LEcya	0.21 ± 0.21	-	-	0.23 ± 0.23	-	-	NS
LElan	0.68 ± 0.31	-	0.18 ± 0.18	-	0.19 ± 0.19	-	NS
WLint	-	-	-	-	37.41 ± 0.19	-	NS
XLboe	0.24 ± 0.24	-	-	-	-	-	NS
FRspp.	0.68 ± 0.31	0.41 ± 0.26	0.18 ± 0.18	-	0.19 ± 0.19	0.51 ± 0.51	NS
NNmus	-	-	0.63 ± 0.63	0.56 ± 0.25	0.7 ± 0.35	-	NS
PRspp.	0.21 ± 0.21	0.39 ± 0.25	1.86 ± 0.75	0.15 ± 0.15	0.37 ± 0.23	-	NS
PTcal	-	-	-	-	0.47 ± 0.47	-	NS
MSspp.	4.29 ± 2.11	4.2 ± 2.11	2.48 ± 0.67	0.63 ± 0.45	0.71 ± 0.45	-	NS

SNele	-	-	-	-	-	0.17 ± 0.17	NS
SNret	-	-	0.2 ± 0.2	-	-	-	NS
KA'4'	-	-	-	-	-	0.13 ± 0.13	NS
SDmal	0.21 ± 0.21	-	0.4 ± 0.26	-	-	-	NS
SPpum	-	-	-	-	0.7 ± 0.35	-	*
DIfus	-	-	-	0.6 ± 0.42	0.17 ± 0.17	-	NS
MGmin	7.54 ± 4.0	7.07 ± 2.78	18.81 ± 15.77	9.69 ± 6.12	3.28 ± 1.94	6.57 ± 4.75	NS

-: Not recorded, NS: p > 0.05, *: p < 0.05, **: p < 0.01

Table 4. Summary data for spring (April '12 and April '13) Collembola mean density (kg-1) per plot ± standard error for both RHS experimental plots separated by vegetation origin, with significance of between treatment effects calculated by the Kruskal-Wallis test. N = Native, Z = Near native, E = Exotic. See Appendix 3.4.2., Table 2., for interpretation of species codes.

	Deer's Farm			Howard's Field			Treatment effect
Taxa	**N**	**Z**	**E**	**N**	**Z**	**E**	
CRthe	0.18 ± 0.18	-	-	-	-	-	NS
DOtig	-	0.18 ± 0.18	1.31 ± 1.31	0.18 ± 0.18	1 ± 1	0.58 ± 0.41	NS
FO spp.	0.18 ± 0.18	4.54 ± 4.54	-	0.34 ± 0.34	3.32 ± 2.28	-	NS
FOspi	-	-	-	-	-	0.36 ± 0.23	NS
IS spp.	1.68 ± 0.67	1.81 ± 1.04	3.96 ± 3.11	2.42 ± 1.18	1.56 ± 0.89	0.39 ± 0.24	NS
IMmin	-	-	-	-	-	0.16 ± 0.16	NS
ITpro	0.18 ± 0.18	1.13 ± 0.74	-	0.35 ± 0.22	-	-	NS
IRpra	-	-	-	-	-	0.17 ± 0.17	NS
MUgar	-	-	-	0.16 ± 0.16	0.51 ± 0.51	-	NS
POnot	57.53 ± 20.27	34.53 ± 6.57	42.01 ± 14.3	49.46 ± 17.77	35.77 ± 6.92	24.38 ± 8.52	NS
ENmul	0.63 ± 0.45	0.69 ± 0.36	-	-	0.16 ± 0.16	0.15 ± 0.15	NS
ENnic	0.18 ± 0.18	-	-	-	-	-	NS
HTmaj	0.59 ± 0.39	1.63 ± 0.77	0.19 ± 0.19	0.33 ± 0.21	0.35	-	NS
LEcya	-	0.36 ± 0.36	0.17 ± 0.17	-	-	-	NS
WLano	-	0.59 ± 0.59	-	-	-	-	NS
CEden	-	-	-	0.16 ± 0.16	-	-	NS
BRpar	-	-	0.19 ± 0.19	-	-	-	NS
FRspp.	1.09 ± 0.57	0.71 ± 0.36	0.34 ± 0.21	0.35 ± 0.35	-	0.16 ± 0.16	NS
PRspp.	0.36 ± 0.36	0.35 ± 0.22	0.58 ± 0.58	-	-	0.16 ± 0.16	NS
PTcal	-	-	0.19 ± 0.19	-	-	-	NS
MSspp.	2.8 ± 0.64	1.93 ± 0.81	4.56 ± 3.24	2.14 ± 0.72	2.42 ± 1.17	1.6 ± 0.84	NS
SNaur	-	0.37 ± 0.37	-	-	-	0.18 ± 0.18	NS
SNele	0.34 ± 0.34	0.33 ± 0.33	0.19 ± 0.19	0.33 ± 0.33	-	0.51 ± 0.51	NS
SNret	-	-	0.77 ± 0.49	-	-	-	NS
KA'4'	-	-	-	-	-	0.3 ± 0.3	NS
KAsch	-	-	-	-	0.16 ± 0.16	0.65 ± 0.41	NS
SDsch	-	0.18 ± 0.18	-	-	-	0.73 ± 0.73	NS
SPpum	-	0.35 ± 0.22	0.58 ± 0.39	-	-	-	NS
BOarv	-	-	-	0.35 ± 0.35	-	0.82 ± 0.82	NS
DEbic	-	-	0.19 ± 0.19	-	-	-	NS
DEpal	3.05 ± 0.91	0.38 ± 0.24	-	0.88 ± 0.69	0.49 ± 0.33	0.69 ± 0.36	NS
MGmin	18.27 ± 11.79	6.4 ± 3.66	7.11 ± 2.65	49.26 ± 16.97	5.13 ± 2.72	6.03 ± 1.47	NS

-: Not recorded, NS: p > 0.05, *: p < 0.05, **: p < 0.01

Table 5. Full results of the two-way ANOVAs on the Shannon-Weiner diversity indices (H') and Gini-Simpson's diversity indices (1-D) with RHS experimental site and planting treatment as factors. Site: Deer's Farm, Howards Field. Treatment: Native, Near native, Exotic.

Index	Factor	F value	d.f.	p value	significance
H'	Site	6.045	1	0.020	*
	Treatment	0.905	2	0.415	NS
	Site:Treatment	0.377	2	0.689	NS
1-D	Site	6.751	1	0.014	*
	Treatment	1.431	2	0.255	NS
	Site:Treatment	0.407	2	0.669	NS

NS: $p > 0.05$, *: $p < 0.05$, **: $p < 0.01$

Table 6. Collembola species/taxa groupings included in the CCAs (Chapter 3.).

Species/taxa grouping	CCA (RHS experimental sites)	CCA (all sites)
Cryptopygus thermophilus	✓	✓
Desoria tigrina	✓	✓
Folsomia candida		
Folsomia quadrioculata group	✓	✓
Folsomia spinosa		
Isotoma spp.	✓	✓
Isotomiella minor		✓
Isotomodes productus	✓	✓
Isotomurus palustris		✓
Isotomurus prasinus		
Mucrosomia garretti	✓	✓
Parisotoma notabilis	✓	✓
Proisotoma minuta		
Proisotoma minima		
Pseudisotoma sensibilis		✓
Tomocerus sp.		✓
Cyphoderus albinus		
Entomobrya intermedia		
Entomobrya marginata		
Entomobrya multifasciata	✓	✓
Entomobrya nicoleti	✓	✓
Entomobrya nivalis		
Heteromurus major	✓	✓
Lepidocyrtus cyaneus	✓	✓
Lepidocyrtus curvicolis		
Lepidocyrtus lanuginosus	✓	✓
Lepidocyrtus lignorum		✓
Orchesella cincta		
Willemia intermedia		
Willemia anopthalma		
Willemia denisi		
Schoettella ununguiculata		✓
Xenylla boerneri		
Ceratophysella denticulata		

Brachystomella parvula		✓
Friesea spp.	✓	✓
Micranurida forsslundi		✓
Micranurida pygmaea		✓
Neanura muscorum	✓	✓
Deuteraphorura inermis		
Onychiurus ambulans		
Protaphorura spp.	✓	✓
Supraphorura furcifera		
Paratullbergia callipygos		✓
Mesaphorura spp.	✓	✓
Sminthurinus aureus		✓
Sminthurinus elegans	✓	✓
Sminthurinus reticulatus		
Katianna species 4		
Katianna schoetti		
Lipothrix lubbocki		✓
Sminthurus nigromaculatus		
Sminthurides malmgreni		
Sminthurides parvulus		
Sminthurides schoetti		✓
Sphaeridia pumilis	✓	✓
Bourletiella arvalis		✓
Bourletiella hortensis		
Deuterosminthurus bicinctus		
Deuterosminthurus pallipes	✓	✓
Deuterosminthurus sulphureus		
Heterosminthurus bilineatus		✓
Dicyrtoma fusca		✓
Dicyrtomina saundersi		✓
Megalothorax minimus	✓	✓

✓: species included, grey shading: not found in the RHS experimental plots

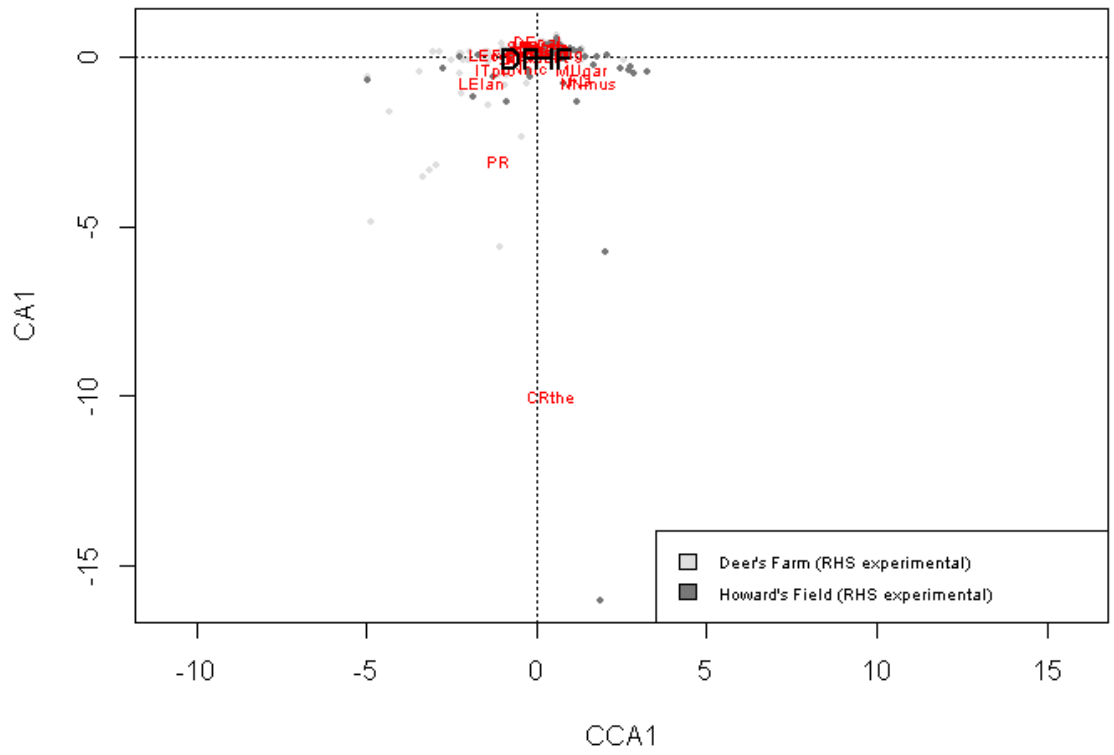

Figure 1. Full CCA ordination diagram of RHS experimental plot main Collembola species abundances (log-transformed) separated by site. Black labels represent site centroids: DF = Deer's Farm and HF = Howard's Field. Red labels are Collembola species codes, see Appendix 3.4.2., Table 2., for interpretation.

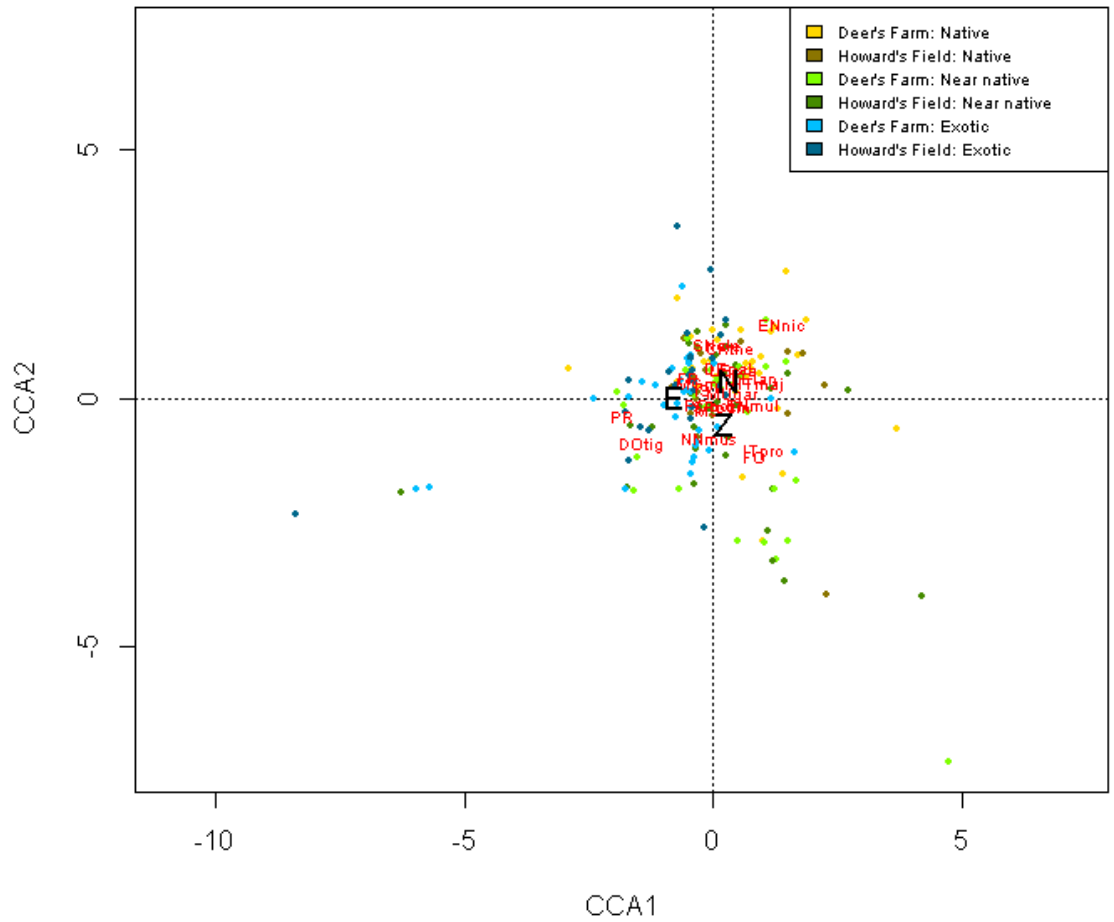

Figure 2. CCA ordination diagram of RHS experimental plot main Collembola species abundances (log-transformed) separated by vegetation treatment. Black labels represent treatment centroids: N = Native, Z = Near native and E = Exotic. Red labels are Collembola species codes, codes, see Appendix 3.4.2., Table 2., for interpretation.

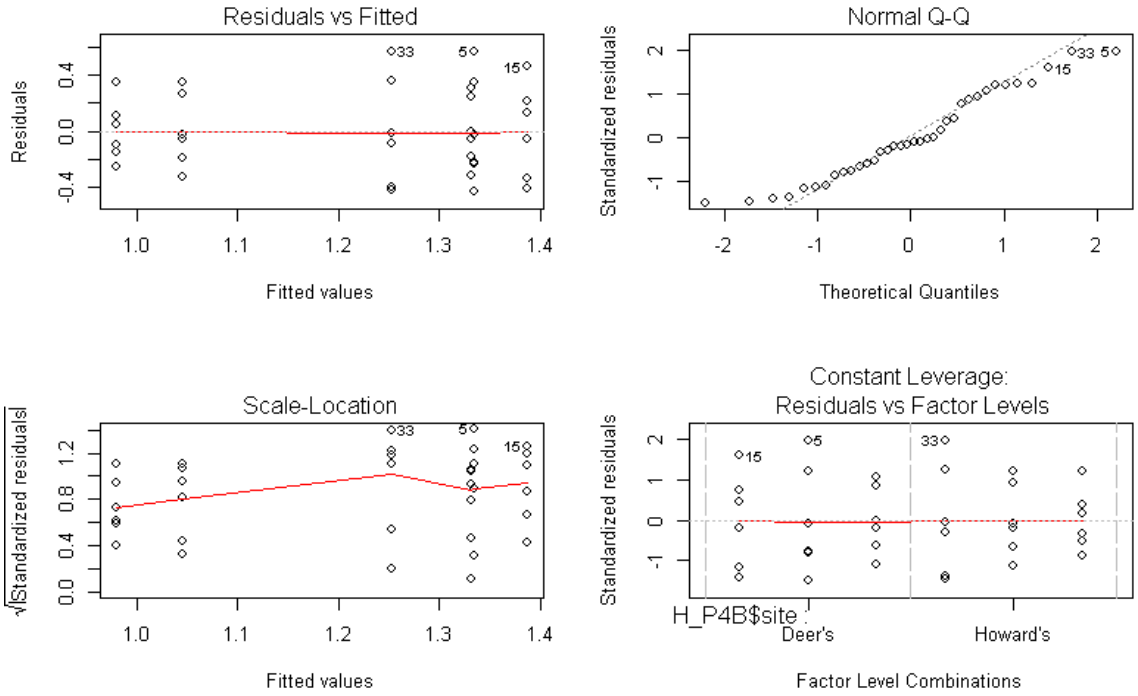

Figure 3. Plots of residuals for two-way ANOVA on H' with RHS experimental site and treatment as factors.

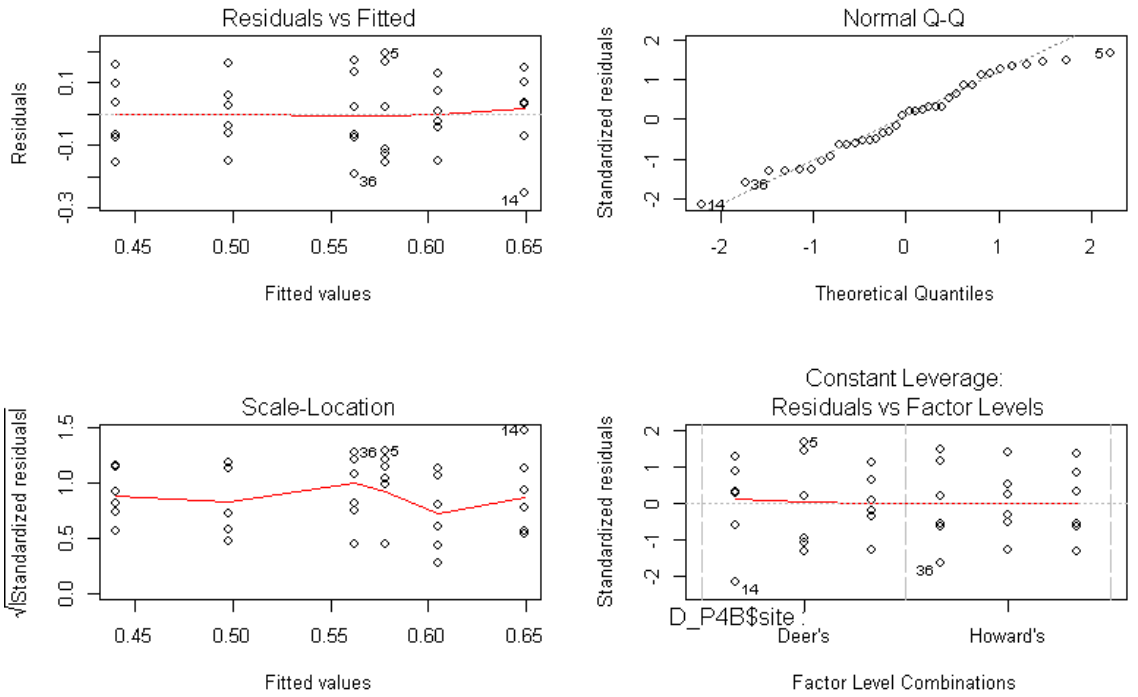

Figure 4. Plots of residuals for two-way ANOVA on 1-D with RHS experimental site and treatment as factors.

Appendix 3.4.5.

Table 1. Metrics of species diversity: Species richness (R), Shannon-Weiner (H') and Gini-Simpson (1-D) for all sites: absolute species richness was calculated per site/treatment and species diversity indices per plot (pooled sampling occasion). One randomly selected soil core per sampling occasion (April '12 - April 13). The numbers of soil cores the figures are derived from are provided.

Site	Site/treatment	Soil cores	Total R	H'	1-D
Deer's Farm	**RHS site**	72	18	1.00 ± 0.07	0.50 ± 0.03
	Adjacent site	24	13	1.60 ± 0.05	0.75 ± 0.02
Deer's Farm	**Native**	24	16	1.12 ± 0.11	0.52 ± 0.05
	Near native	24	13	1.03 ± 0.12	0.50 ± 0.06
	Exotic	24	11	0.85 ± 0.11	0.48 ± 0.06
Howard's Field	**RHS site**	72	26	0.88 ± 0.11	0.41 ± 0.05
	Adjacent site	24	19	1.75 ± 0.09	0.72 ± 0.04
Howard's Field	**Native**	24	19	0.93 ± 0.22	0.43 ± 0.10
	Near native	24	16	0.65 ± 0.17	0.29 ± 0.07
	Exotic	24	16	1.06 ± 0.14	0.52 ± 0.06
Wisley Common		24	28	1.79 ± 0.07	0.72 ± 0.03
Buxton Wood		24	19	1.67 ± 0.08	0.74 ± 0.02

Table 2. Summary data for Collembola mean density (kg-1) per site ± standard error, with significance of between site effects calculated by the Kruskal-Wallis test. See Appendix 3.4.2., Table 3., for interpretation of species codes.

	Deer's Farm	Howards Field	Deer's Adjacent	Howard's Adjacent	Wisley Common	Buxton Wood	Site effect
CRthe	0.03 ± 0.03	-	29.3 ± 9.26	89.45 ± 24.82	-	-	***
DOtig	0.22 ± 0.19	0.26 ± 0.15	-	0.36 ± 0.36	-	-	NS
FOcan	-	-	-	-	0.46 ± 0.46	-	NS
FOspp.	0.67 ± 0.64	0.69 ± 0.4	-	0.94 ± 0.6	73.76 ± 12.72	39.93 ± 7.8	***
FOspi	-	0.07 ± 0.04	-	-	-	-	NS
ISspp.	1.41 ± 0.46	1.01 ± 0.43	26.61 ± 6.88	20.59 ± 4.93	0.53 ± 0.45	0.09 ± 0.09	***
IMmin	-	0.07 ± 0.04	-	-	2.91 ± 1.25	3.63 ± 0.85	***
ITpro	0.77 ± 0.42	0.1 ± 0.06	15.28 ± 13.08	17.33 ± 8.51	-	-	**
Irpal	-	-	-	-	2.84 ± 1.22	-	***
IRpra	-	0.02 ± 0.02	-	-	0.1 ± 0.1	-	NS
MUgar	0.03 ± 0.03	0.14 ± 0.09	-	-	-	-	NS
POnot	31.52 ± 5.03	35.57 ± 5.46	7.4 ± 3.01	3.21 ± 1.35	7.57 ± 2.7	39.72 ± 2.99	***
PImin	-	-	-	-	-	0.09 ± 0.09	NS
PEsen	-	-	-	-	21.99 ± 3.83	0.09 ± 0.09	***
TOsp.	-	-	-	-	0.44 ± 0.22	-	***
CYalb	-	-	-	0.72 ± 0.43	-	-	***
ENint	0.02 ± 0.02	-	-	-	-	-	NS
ENmar	-	-	-	-	0.09 ± 0.09	-	NS
ENmul	0.83 ± 0.21	0.43 ± 0.13	0.25 ± 0.17	-	1.59 ± 0.17	-	***
ENnic	0.08 ± 0.04	0.07 ± 0.07	-	-	1.43 ± 0.33	-	***
Enniv	-	-	-	-	0.06 ± 0.06	-	NS

HTmaj	1.12 ± 0.31	0.59 ± 0.26	1.72 ± 0.57	1.7 ± 0.54	-	-	**
LEcya	0.12 ± 0.07	0.03 ± 0.03	3.18 ± 0.88	0.1 ± 0.1	0.71 ± 0.48	-	***
LEcur	-	-	-	-	0.07 ± 0.07	0.09 ± 0.09	NS
LElan	0.25 ± 0.11	0.02 ± 0.02	0.81 ± 0.33	-	11.6 ± 1.89	2.53 ± 0.6	***
LElig	-	-	-	-	0.37 ± 0.19	2.2 ± 0.84	***
ORcin	-	-	-	-	-	0.09 ± 0.09	NS
WLint	-	4.88 ± 4.88	-	-	-	-	NS
WLano	0.07 ± 0.07	-	-	-	0.07 ± 0.07	-	NS
WLden	-	-	-	-	0.1 ± 0.1	-	NS
SHung	-	-	-	-	1.6 ± 1.12	-	**
XLboe	0.03 ± 0.03	-	-	0.1 ± 0.1	-	-	NS
CEden	-	0.02 ± 0.02	-	-	0.07 ± 0.07	-	NS
BRpar	0.05 ± 0.04	-	3.38 ± 0.72	6.74 ± 1.51	-	-	***
FRspp.	0.77 ± 0.25	0.27 ± 0.2	1.07 ± 0.96	6.46 ± 1.59	3.62 ± 2.06	15.07 ± 9.1	***
MIfor	-	-	-	-	0.5 ± 0.29	0.79 ± 0.27	***
MIpyg	-	-	-	-	0.99 ± 0.42	1.6 ± 1.05	***
NNmus	0.08 ± 0.08	0.26 ± 0.26	-	-	0.15 ± 0.15	0.16 ± 0.1	NS
DUine	-	-	-	-	-	0.09 ± 0.09	NS
PRspp.	0.6 ± 0.2	0.09 ± 0.04	-	3.38 ± 1.36	-	3.36 ± 1.77	**
SRfur	-	-	-	-	-	0.09 ± 0.09	NS
PTcal	0.03 ± 0.03	0.06 ± 0.06	-	-	0.15 ± 0.09	0.18 ± 0.12	NS
MSspp.	3.26 ± 0.54	1.42 ± 0.31	6.46 ± 1.5	10.62 ± 1.52	4.95 ± 0.77	7.81 ± 0.72	***
SNaur	0.05 ± 0.05	0.05 ± 0.05	0.11 ± 0.11	0.9 ± 0.9	0.92 ± 0.23	0.64 ± 0.42	**
SNele	0.2 ± 0.09	0.34 ± 0.19	0.92 ± 0.38	5.06 ± 1.06	0.23 ± 0.16	-	***
SNret	0.13 ± 0.09	-	-	-	-	-	NS
KA'4'	-	0.06 ± 0.04	-	-	-	-	NS
KAsch	-	0.1 ± 0.06	-	-	-	-	NS
LIlub	-	-	-	-	0.66 ± 0.46	-	**
SMnig	-	-	-	-	0.13 ± 0.08	-	**
SDmal	0.08 ± 0.04	-	-	-	-	-	NS
SDpar	-	-	-	-	0.1 ± 0.1	-	NS
SDsch	0.03 ± 0.03	0.1 ± 0.1	-	-	0.25 ± 0.16	-	NS
SPpum	0.26 ± 0.1	0.18 ± 0.07	16.62 ± 4	19.07 ± 4.42	1.26 ± 0.86	-	***
BOarv	-	0.16 ± 0.12	1 ± 0.33	0.69 ± 0.31	-	-	***
BOhor	-	0.02 ± 0.02	-	-	-	-	NS
DEbic	0.03 ± 0.03	-	0.35 ± 0.35	-	-	-	NS
DEpal	0.57 ± 0.21	0.57 ± 0.24	1.09 ± 0.6	3.2 ± 2.17	-	-	*
DEsul	-	-	-	0.1 ± 0.1	-	-	NS
HSbil	-	-	-	-	0.6 ± 0.21	-	***
DIfus	-	0.1 ± 0.06	-	-	0.39 ± 0.18	0.18 ± 0.11	*
DMsau	-	-	-	-	0.16 ± 0.11	0.23 ± 0.15	**
MGmin	9.56 ± 2.4	11.72 ± 3.43	-	-	4.66 ± 2.03	14.73 ± 1.75	***

-: Not recorded, NS: $p > 0.05$, *: $p < 0.05$, **: $p < 0.01$

Table 3. Deer's Farm combined species richness. For the subset of data collected between April '12 and April '13 with one soil core per sampling occasion: grand total 22 species.

	Deer's Native	Deer's Near native	Deer's Exotic
Deer's Near native	17		
Deer's Exotic	17	14	
Deer's Adjacent	21	18	18

Table 4. Howard's Field combined total species richness. For the subset of data collected between April '12 and April '13 with one soil core per sampling occasion: grand total 31 species.

	Howard's Native	Howard's Near native	Howard's Exotic
Howard's Near native	21		
Howard's Exotic	25	22	
Howard's Adjacent	26	27	27

Table 5. Full results of the one-way ANOVA and Kruskal-Wallis tests on the Shannon-Weiner diversity indices (H'), with site as the independent variable (Site: Deer's Farm RHS experimental site, Howard's Field RHS experimental site, Deer's Farm adjacent, Howard's Field adjacent, Wisley Common and Buxton Wood).

Test	Factor	F value	Chi-squared	d.f.	p value	significance
ANOVA	Site	16.16	NA	5	9.96e-10	***
Kruskal-Wallis	Site	NA	37.23	5	5.38e-7	***

NS: $p > 0.05$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$

Table 6. Tukey's HSD post-hoc test results: p values for multiple comparisons of Shannon-Weiner diversity indices between sites. *'s denote results were there was a significant difference. DF: Deer's Farm RHS experimental plots, HF: Howard's Field RHS experimental plots, DFA: Deer's Farm adjacent, HFA: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood.

	HF	DF	DFA	HFA	H
DF	**p > 0.05**				
DFA	**p < 0.001 *** **	**p < 0.01 ****			
HFA	**p < 0.001 *** **	**p < 0.001 *** **	**p > 0.05**		
H	**p < 0.001 *** **	**p < 0.001 *** **	**p > 0.05**	**p > 0.05**	
W	**p < 0.001 *** **	**p < 0.001 *** **	**p > 0.05**	**p > 0.05**	**p > 0.05**

Table 7. Dunn's post-hoc test results: Z statistics and p values for multiple comparisons of Shannon-Weiner diversity indices between sites. *'s denote results were there was a significant difference. DF: Deer's Farm RHS experimental plots, HF: Howard's Field RHS experimental plots, DFA: Deer's Farm adjacent, HFA: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood.

	HF	DF	DFA	HFA	H
DF	**Z = 0.39** **p = 1**				
DFA	**Z = 3.05** **p < 0.05 ***	**Z = 2.77** **p < 0.05 ***			
HFA	**Z = 3.82** **p < 0.01 ****	**Z = -3.54** **p < 0.01 ****	**Z = -0.63** **p = 1**		
H	**Z = 3.72** **p < 0.01 ****	**Z = -3.44** **p < 0.01 ****	**Z = -0.54** **p = 1**	**Z = -0.08** **p = 1**	
W	**Z = -3.50** **p < 0.01 ****	**Z = -3.22** **p < 0.01 ****	**Z = -0.36** **p = 1**	**Z = 0.26** **p = 1**	**Z = 0.18** **p = 1**

Table 8. Full results of the one-way ANOVA and Kruskal-Wallis tests on the Gini-Simpson diversity indices (1-D), with site as the independent variable (Site: Deer's Farm RHS experimental site, Howard's Field RHS experimental site, Deer's Farm adjacent, Howard's Field adjacent, Wisley Common and Buxton Wood).

Test	Factor	F value	Chi-squared	d.f.	p value	significance
ANOVA	Site	11.19	NA	5	1.99e-7	***
Kruskal-Wallis	Site	NA	33.97	5	2.41e-6	***

NS: p > 0.05, *: p < 0.05, **: p < 0.01, ***: p < 0.001

Table 9. Tukey's HSD post-hoc test results: p values for multiple comparisons of Gini-Simpson diversity indices between sites. DF: Deer's Farm RHS experimental plots, HF: Howard's Field RHS experimental plots, DFA: Deer's Farm adjacent, HFA: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood.

	HF	DF	DFA	HFA	H
DF	**p > 0.05**				
DFA	**p < 0.001 ***	**p < 0.01 ****			
HFA	**p < 0.001 ***	**p < 0.05 ***	**p > 0.05**		
H	**p < 0.001 ***	**p < 0.05 ***	**p > 0.05**	**p > 0.05**	
W	**p < 0.001 ***	**p < 0.01 ****	**p > 0.05**	**p > 0.05**	**p > 0.05**

NS: p > 0.05, *: p < 0.05, **: p < 0.01, ***: p < 0.001

Table 10. Dunn's post-hoc test results: Z statistics and p values for multiple comparisons of Gini-Simpson diversity indices between sites. *'s denote results were there was a significant difference. DF: Deer's Farm RHS experimental plots, HF: Howard's Field RHS experimental plots, DFA: Deer's Farm adjacent, HFA: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood.

	HF	DF	DFA	HFA	H
DF	**Z = 0.67** **NS**				
DFA	**Z = 3.71** **p < 0.01 ****	**Z = 3.24** **p < 0.01 ****			
HFA	**Z = 3.29** **p < 0.01 ****	**Z = -2.81** **p < 0.05 ***	**Z =0.35** **NS**		
H	**Z = 3.16** **p < 0.05 ***	**Z = -2.69** **NS (p = 0.053)**	**Z = 0.45** **NS**	**Z = -0.1** **NS**	
W	**Z = -3.67** **p < 0.01 ****	**Z = -3.20** **p < 0.05 ***	**Z = 0.03** **NS**	**Z = -0.31** **NS**	**Z = -0.41** **NS**

NS: p > 0.05, *: p < 0.05, **: p < 0.01, ***: p < 0.001

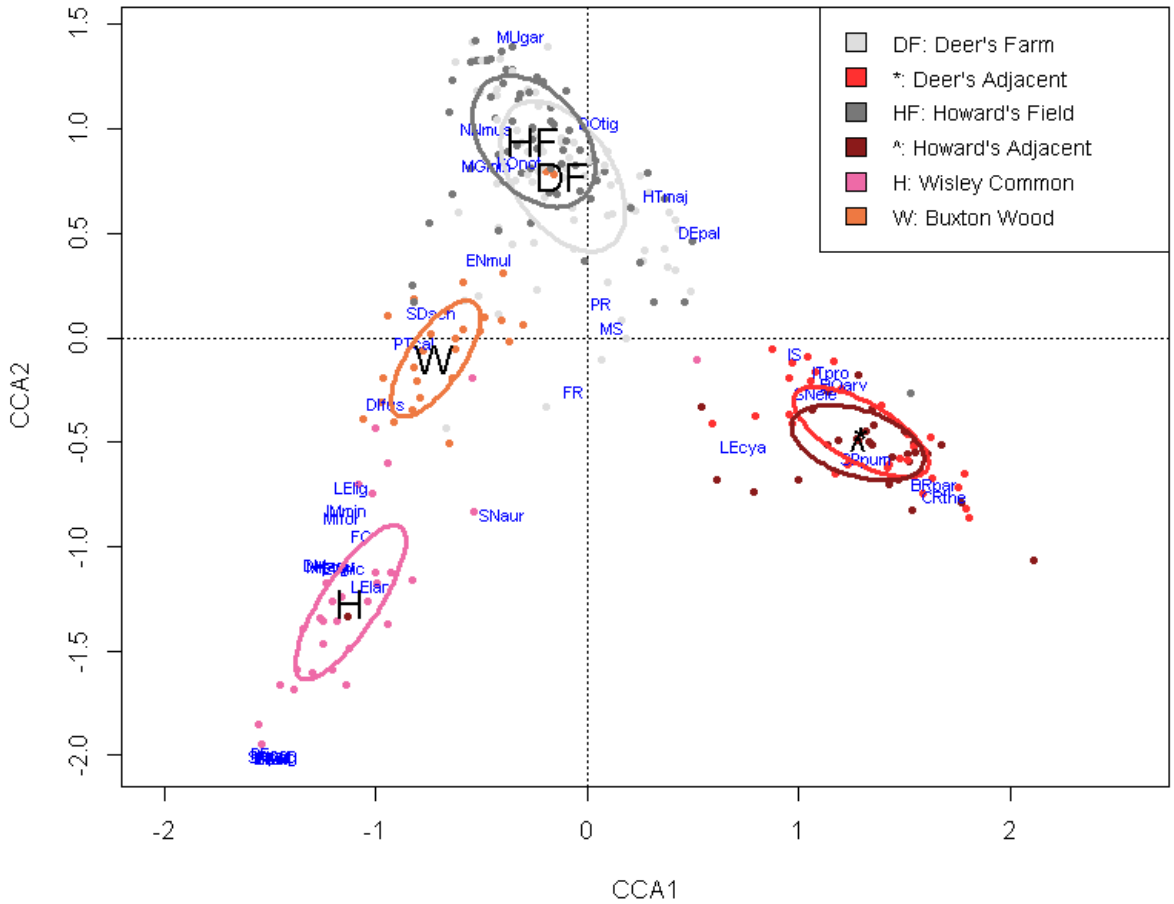

Figure 1. Full CCA ordination diagram of main Collembola species abundances (log-transformed) separated by site. Black labels represent treatment centroids: DF = Deer's Farm (RHS experimental plots), HF = Howard's Field (RHS experimental plots) * = Deer's Farm adjacent site, ^ = Howard's Field adjacent site, H = Wisley Common and W = Buxton Wood. Ellipses plotted using standard deviation from the centroids. Blue labels are Collembola species codes, codes, see Appendix 3.4.2., Table 2., for interpretation.

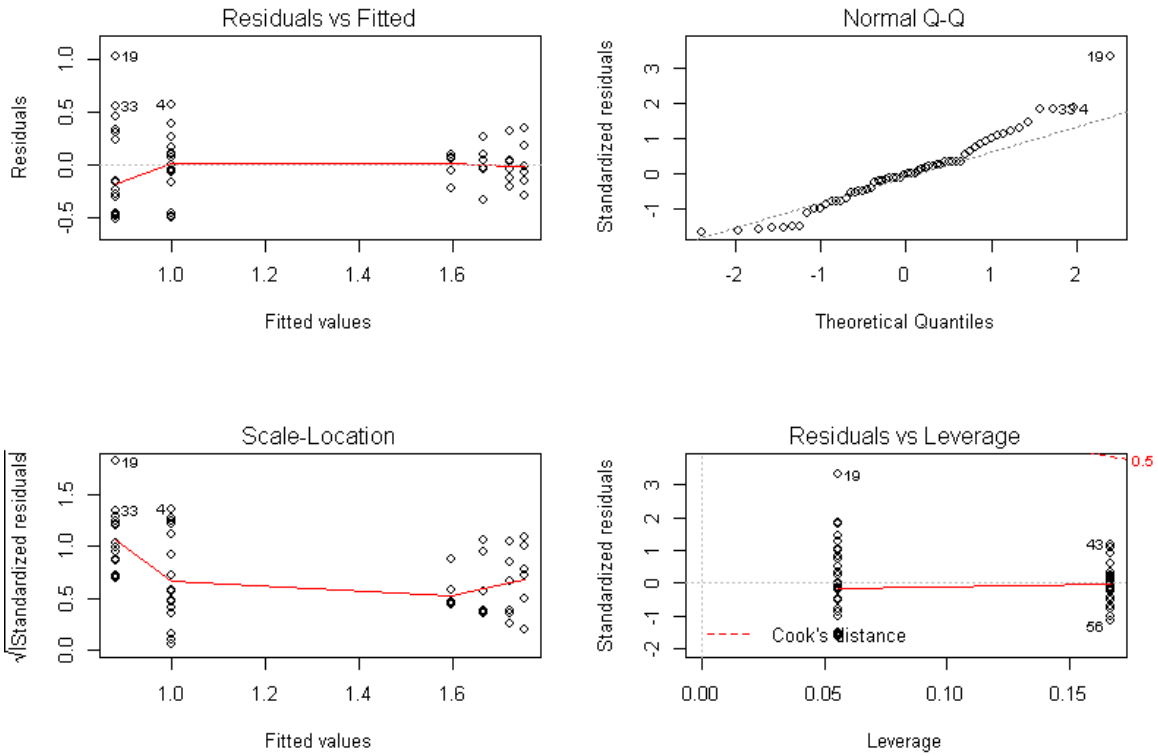

Figure 2. Plots of residuals for the one-way ANOVA on H' with 'site' as the independent variable.

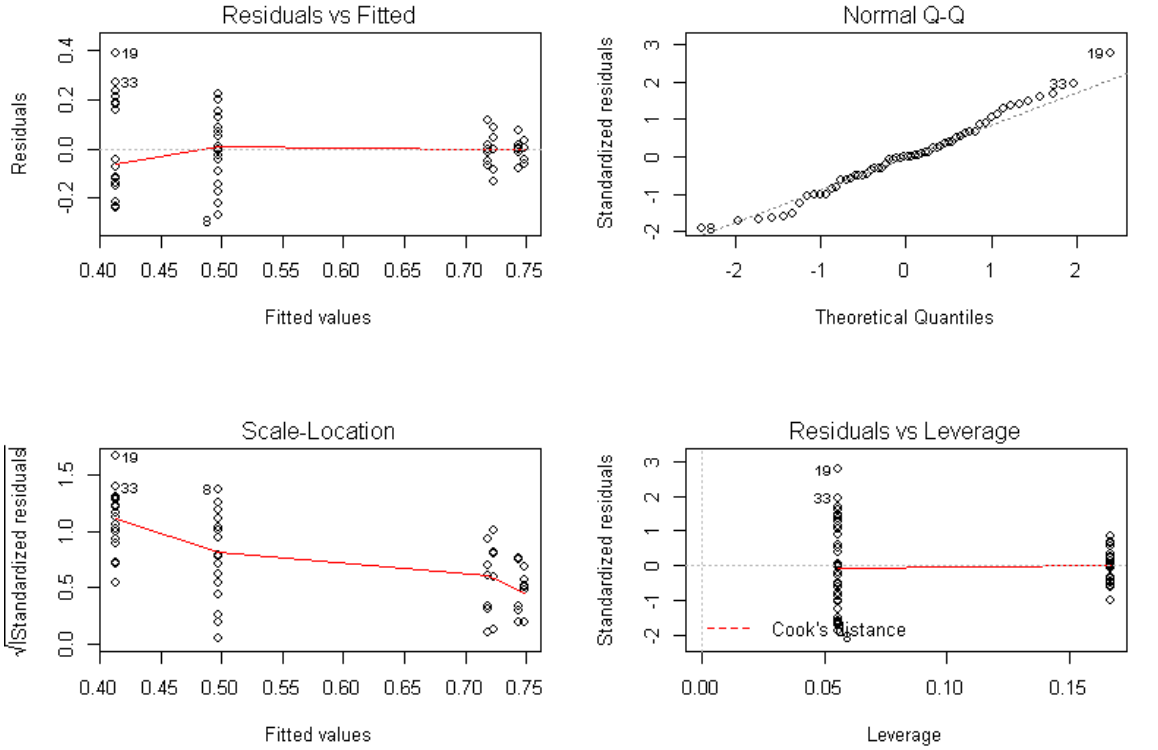

Figure 3. Plots of residuals for the one-way ANOVA on 1-D with 'site' as the independent variable.

Appendix 4.2.

Table 1. Collembola species retrieved during the Oct '12 sampling occasion and the origin (site/treatment) of the specimens used to represent them, plot codes follow those in Appendix 3.2. (Figures 1. - 7.). See Appendix 3.4.2., Table 2., for interpretation of species codes. Cells shaded light grey indicate where samples were not processed for molecular work, dark grey shading indicates where sampling was unsuccessful.

Species code	Abundance (All sites)	Abundance (RHS plots)	Specimen origin						
			1	2	3	4	5	6	7
CRthe	200	-	HA4						
FOman	7	6	W3						
FO	208	-	NA						
FOspi	1	1	H5ZB						
ISang	13	-	DA1						
IMmin	21	2	H2						
ITpro	192	16	HA6						
IRpal	3	-	H4						
IRpra	1	-	H2						
MUgar	2	2	H4NC						
POnot	412	285	D5NB	D1EB	H3NC	H1ZA	DA4	H3	W6
PImin	1	-	W3						
PEsen	38	-	H6						
CYalb	1	-	HA3						
ENint	1	1	D5EB						
ENmar	1	-	H3						
ENmul	15	12	D5NB						
ENnic	2	-	H6						
HTmaj	10	10	D4NA						
LEcya	2	2	D6NC	D6NC					
LElan	25	2	H6						
LElig	27	-	W5	H6					
ORcin	1	-	W6						
WLint	202	202	H2ZB						
SHung	1	-	H3						
BRpar	22	-	HA3						
FRcla	2	1	HA2						
FRmir	1	1	H2ZB						
FRtru	7	2	HA2						
FR	79	-	NA						
MIfor	5	-	W6						
MIpyg	12	-	W1						
NNmus	6	5	H1NA						
DUine	1	-	W1						
PR	37	4	NA						
PRarm	5	2	D1EB	H2ZB	W6				
PTcal	4	3	W4						
MSmac	13	5	DA4	HA4					
MS	102	39	NA						

SNaur	8	-	W5	H5
SNele	11	-	DA3	HA4
SNret	1	1	D3EA	
KA'4'	1	1	D5EB	
LIlub	2	-	H1	
SMnig	1	-	H5	
SDmal	3	3	D6NC	D1EB
SDsch	2	-	H1	
SPpum	52	4	DA3	DA4
BOarv	1	-	DA5	
DEpal	1	-	DA3	
DIfus	8	4	H2	H2NB
DMsau	3	-	W2	
MGmin	262	209	D5NB	D1EB
Anuraphorinae *	2	2		
EN *	10	5		
LE *	1	-		
Entomobryidae *	6	1		
SN *	2	1		
Symphypleona *	1	-		
Mangled *	1	1		

* : mangled, - : taxa not present

Table 2. ColFolmer primer base sequences.

Direction	Base sequence (5' to 3')																								
Forward	T	T	T	C	A	A	C	A	A	A	T	C	A	T	A	A	R	G	A	Y	A	T	Y	G	G
Reverse	T	A	A	A	C	T	T	C	N	G	G	R	T	G	N	C	C	A	A	A	A	A	A	T	C	A

Appendix 4.3.

Table 1. Accession numbers and collection details for sequences downloaded from GenBank. See Appendix 3.4.2., Table 2., for interpretation of species codes.

Species	GenBank Acc. number	BOLD ID	Photo	Collector	Associated publication reference
SHung	HQ732079	GBCO1606-13.COI-5P	NA	NA	Greenslade et al. (2011)
ENmar	NA	GENHP1212-12.COI-5P	✓	Porco	NA

MrBayes code block

```
begin mrbayes;
outgroup Protura;
[!MrBayes settings for the best-fit model (GTR+I+G) selected by AIC in MrModeltest 2.2]
        Prset statefreqpr=dirichlet(1,1,1,1);
        Lset nst=6 rates=invgamma;
mcmc nruns=2 nchains=4ngen=100000samplefreq=100printfreq=100
filename=Plantsforbugs savebrlens=yes;
sump burnin=0 nruns=2;
sumt burnin=0 nruns=2 ntrees=1;
end;
```

Table 2. Clump specifications in 'sample' file for analysis in Phylocom. Plot codes follow those in Appendix 3.2. (Figures 1. - 7.). See Appendix 3.4.2., Table 2., for interpretation of species codes.

Plot code	Plot abundance	Species code
D5NB	14	POnot
D5NB	3	MGmin
D5NB	2	ENmul
D3NA	9	MSmac
D3NA	4	POnot
D3NA	4	MGmin
D3NA	3	ITpro
D1NB	1	POnot
D1NB	1	MGmin
D2NC	19	MGmin
D2NC	12	POnot
D2NC	5	MSmac
D2NC	5	HTmaj
D2NC	4	ENmul
D6NC	7	POnot
D6NC	1	LElan
D6NC	1	LEcya
D6NC	1	MSmac
D6NC	1	SDmal
D4NA	7	POnot
D4NA	5	MGmin
D4NA	4	HTmaj
D4NA	1	ENmul
D4NA	1	LElan

D4NA	1	FRcla
D1ZB	13	POnot
D1ZB	9	MGmin
D1ZB	5	MSmac
D3ZA	16	MGmin
D3ZA	4	POnot
D5ZB	5	POnot
D5ZB	4	MGmin
D5ZB	1	ENmul
D5ZB	1	MSmac
D2ZC	4	MSmac
D2ZC	2	ITpro
D2ZC	1	POnot
D4ZA	11	ITpro
D4ZA	7	POnot
D4ZA	6	MSmac
D4ZA	1	PRarm
D4ZA	1	MGmin
D6ZC	3	MGmin
D1EB	6	MGmin
D1EB	5	POnot
D1EB	1	PRarm
D1EB	1	SDmal
D3EA	2	ENmul
D3EA	1	PRarm
D3EA	1	POnot
D3EA	1	MGmin
D3EA	1	SNret
D5EB	2	MSmac
D5EB	1	POnot
D5EB	1	ENint
D6EC	1	MSmac
D4EA	63	MGmin
D4EA	17	POnot
D4EA	2	MSmac
D2EC	3	POnot
D2EC	1	MSmac
D2EC	1	SDmal
H1NA	32	MGmin
H1NA	4	POnot
H1NA	2	MUgar
H1NA	2	DIfus
H1NA	1	NNmus
H5NB	5	POnot
H5NB	2	MGmin
H3NC	13	POnot
H3NC	3	MGmin
H3NC	1	HTmaj

H3NC	1	PRarm
H3NC	1	IMmin
H2NB	4	MGmin
H2NB	3	POnot
H2NB	1	NNmus
H2NB	1	DIfus
H6NA	14	POnot
H6NA	7	MGmin
H6NA	1	ENmul
H6NA	1	NNmus
H6NA	1	MSmac
H4NC	19	POnot
H4NC	2	MSmac
H5ZB	14	POnot
H5ZB	1	FOspi
H5ZB	1	NNmus
H5ZB	1	PRarm
H5ZB	1	MGmin
H3ZC	33	POnot
H3ZC	6	FOman
H3ZC	3	PTcal
H1ZA	6	POnot
H1ZA	2	MSmac
H1ZA	1	ENmul
H1ZA	1	NNmus
H1ZA	1	SPpum
H1ZA	1	IMmin
H1ZA	1	MGmin
H2ZB	202	WLint
H2ZB	14	POnot
H2ZB	2	MSmac
H2ZB	1	PRarm
H2ZB	1	FRmir
H4ZC	18	POnot
H4ZC	2	SPpum
H4ZC	2	MGmin
H4ZC	1	DIfus
H6ZA	8	POnot
H6ZA	1	SPpum
H6ZA	1	MGmin
H3EC	6	MGmin
H3EC	5	POnot
H1EA	5	POnot
H5EB	3	MGmin
H5EB	1	POnot
H5EB	1	KA’4’
H4EC	12	MGmin
H4EC	11	POnot

H2EB		10	POnot
H2EB		2	FRtru

Table 3. The origin of the specimens unidentified to species level (and so excluded from the Table 2. 'sample' file) retrieved during the October '12 sampling.

RHS experimental site	Vegetation origin treatment	Number	Identification notes
Deer's Farm	Native	1	1 juvenile Entomobryidae (mangled)
	Near native	0	
	Exotic	2	1 E*ntomobrya* sp., 1 Anurophinae (mangled)
Howard's Field	Native	5	4 E*ntomobrya* sp., 1 juvenile Anurophinae
	Near native	1	1 *Sminthurinus* sp.
	Exotic	1	1 Anurophinae (mangled)

Appendix 4.4.

Table 1. Collembola sequencing results: the number of COI sequences obtained per species from this research and current (June 2015) availability of molecular sequences on GenBank. See Appendix 3.4.2., Table 2., for interpretation of species codes. Grey shaded areas indicate where no sequences were available.

Species code	COI sequences	Notes	GenBank gene region availability				
			COI	28S	18S	Cytb	Other
CRthe	1						
FOman	1						
FOspi	1	Unable to build consensus seq					
ISang	1		✓	✓	✓		✓
IMmin	1		✓	✓	✓		✓
ITpro	1						
IRpal	1		✓	✓	✓		✓
IRpra	1						
MUgar	1						
POnot	7	Unable to build consensus seq for 1 specimen	✓	✓	✓		✓
PImin	1						
PEsen	1		✓	✓	✓		✓
CYalb	1					✓	
ENint	1		✓				
ENmar	0		✓	✓			✓
ENmul	1		✓	✓	✓		✓
ENnic	1						
HTmaj	1		✓	✓	✓		✓
LEcya	2		✓				✓
LElan	1		✓				✓
LElig	2		✓	✓			✓
ORcin	1		✓	✓	✓	✓	✓
WLint	1						
SHung	0		✓	✓			✓
BRpar	1			✓			
FRcla	1						
FRmir	1						
FRtru	1						
MIfor	1						
MIpyg	1			✓			
NNmus	1		✓	✓	✓		✓
DUine	1						
PRarm	3		✓	✓			✓
PTcal	1						
MSmac	2			✓			
SNaur	2	Read of trace files better for B					
SNele	2		✓				
SNret	1						
KA'4'	1						
LIlub	1		✓	✓			✓

SMnig	1		
SDmal	2	Unable to build consensus seq for 1 specimen	✓
SDsch	0		
SPpum	2	One seq with many ambiguous bases	✓ ✓
BOarv	0		
DEpal	1		
DIfus	2		✓ ✓ ✓
DMsau	1		✓ ✓ ✓
MGmin	2	Read of trace files better for A	✓ ✓ ✓ ✓

Table 2. Full results of the two-way ANOVA on PD and MPD with RHS experimental site and planting treatment as factors. Site: Deer's Farm, Howards Field. Treatment: Native, Near native, Exotic (error = 30 d.f.).

Index	Factor	F value	d.f.	p value	significance
PD	Site	0.002	1	0.962	NS
	Treatment	2.888	2	0.071	NS
	Site:Treatment	3.984	2	0.029	*
MPD	Site	2.375	1	0.134	NS
	Treatment	1.066	2	0.375	NS
	Site:Treatment	0.019	2	0.981	NS

NS: $p > 0.05$, *: $p < 0.05$, **: $p < 0.01$

Table 3. Full results of the two-way ANOVA on PD with RHS experimental site and planting treatment as factors. Site: Deer's Farm, Howards Field. Treatment: Native, Near native, Exotic (interaction term removed, so error = 32 d.f.)

Index	Factor	F value	d.f.	p value	significance
PD	Site	0.002	1	0.965	NS
	Treatment	2.434	2	0.104	NS

NS: $p > 0.05$, *: $p < 0.05$, **: $p < 0.01$

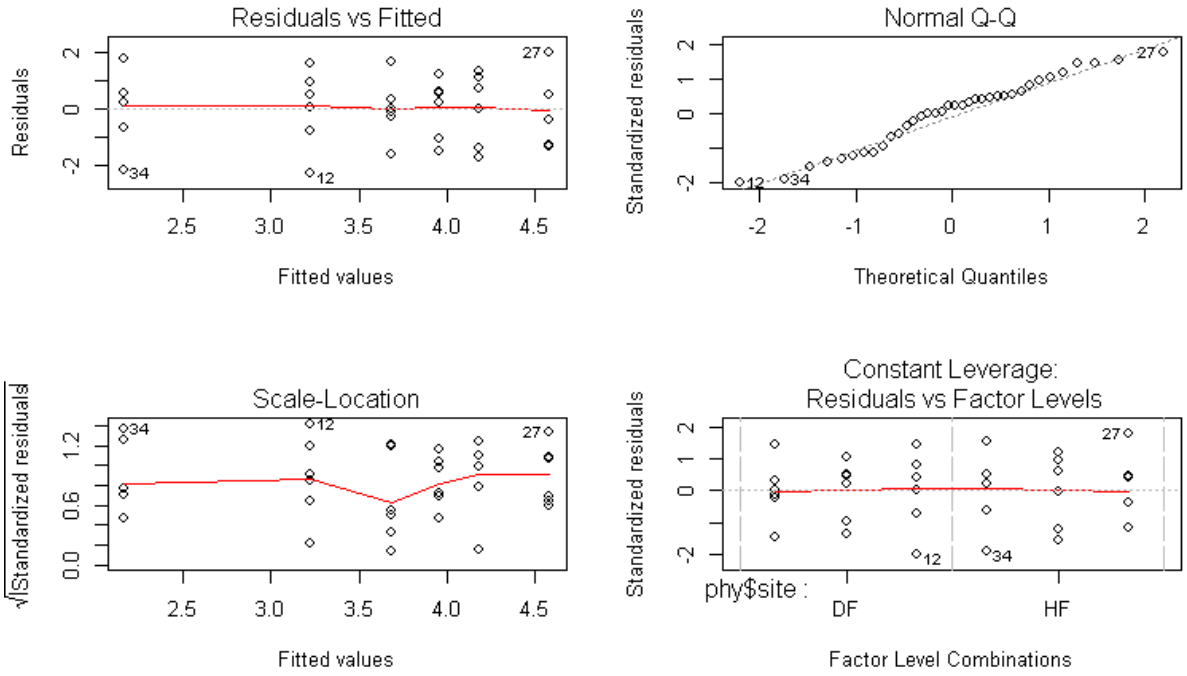

Figure 1. Plots of residuals for two-way ANOVA on PD with RHS experimental site and vegetation origin treatment as factors.

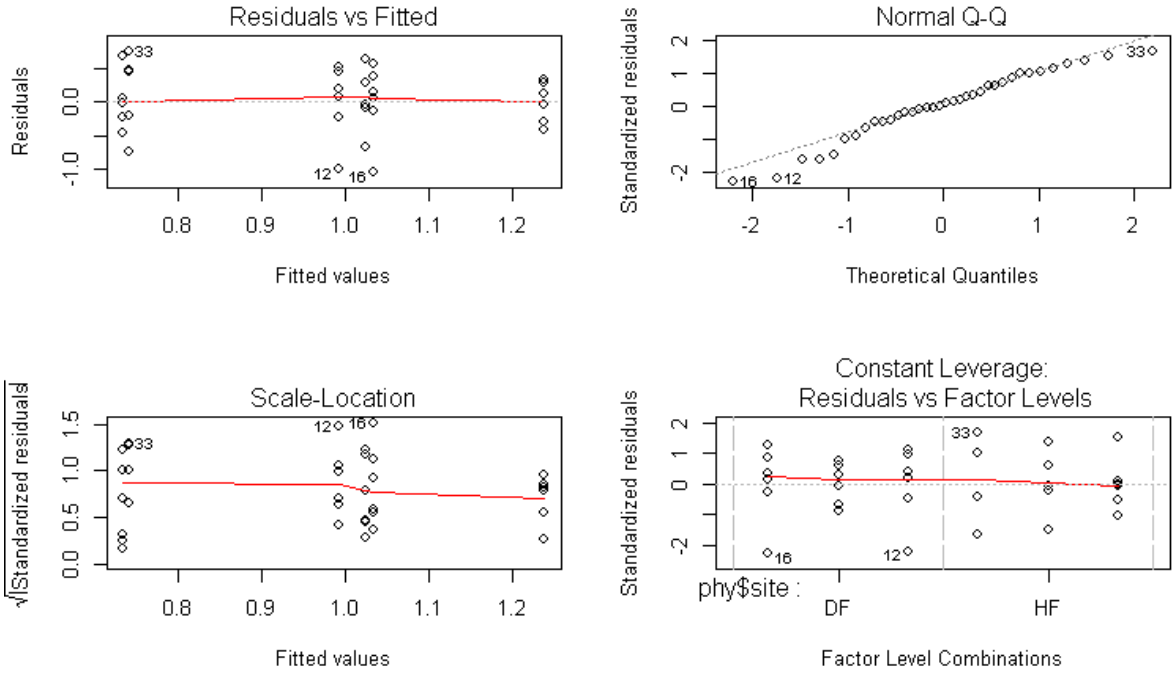

Figure 2. Plots of residuals for the two-way ANOVA on MPD with RHS experimental site and vegetation origin treatment as factors.

Appendix 5.2.

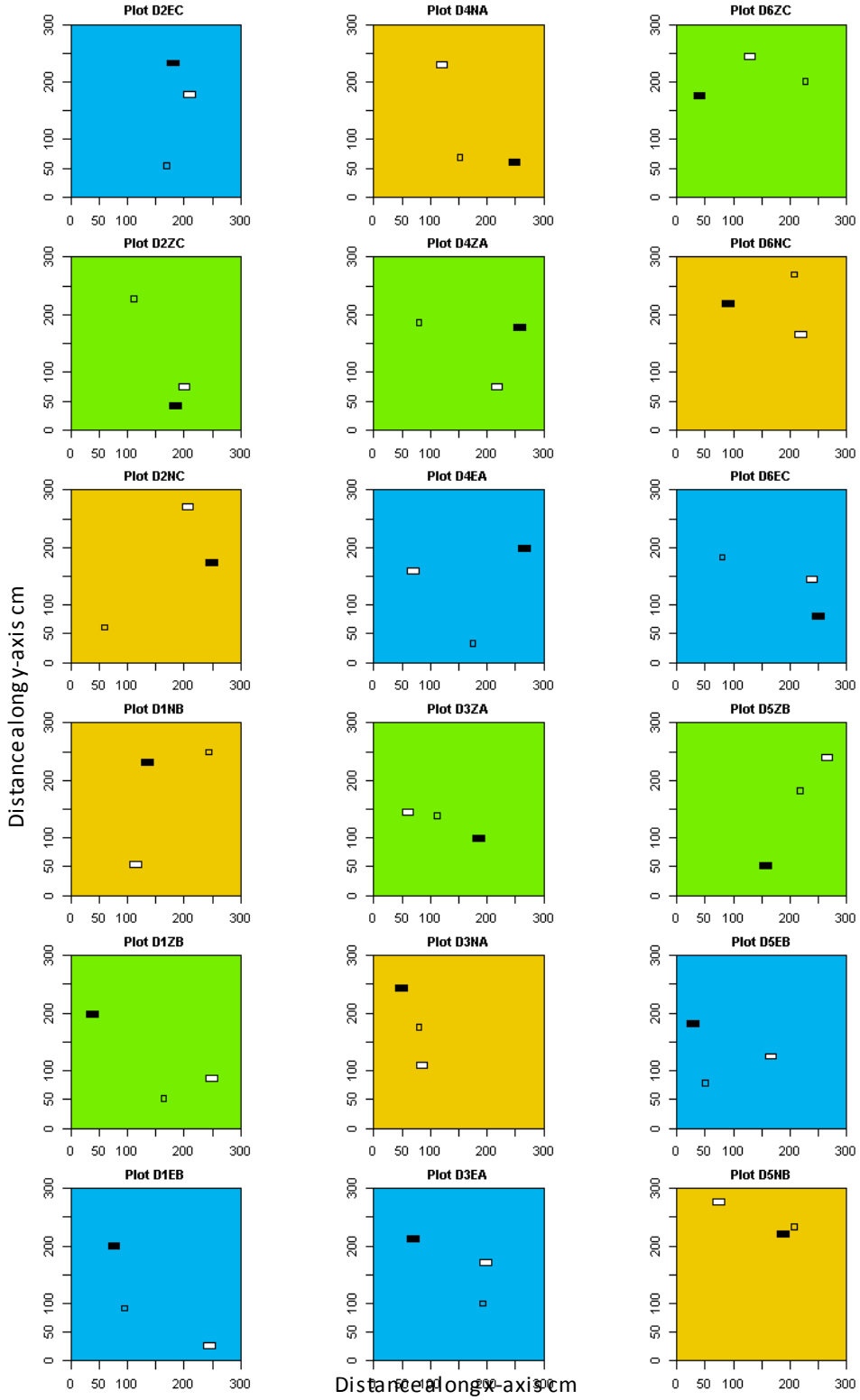

Figure 1. Deer's Farm position of litter bags and bait lamina strips in the RHS experimental plots: black rectangles: twig litter bags, white rectangles: leaf litter bags, unfilled squares: bait lamina strips. Yellow: Native plots, green: Near native plots and blue: Exotic plots.

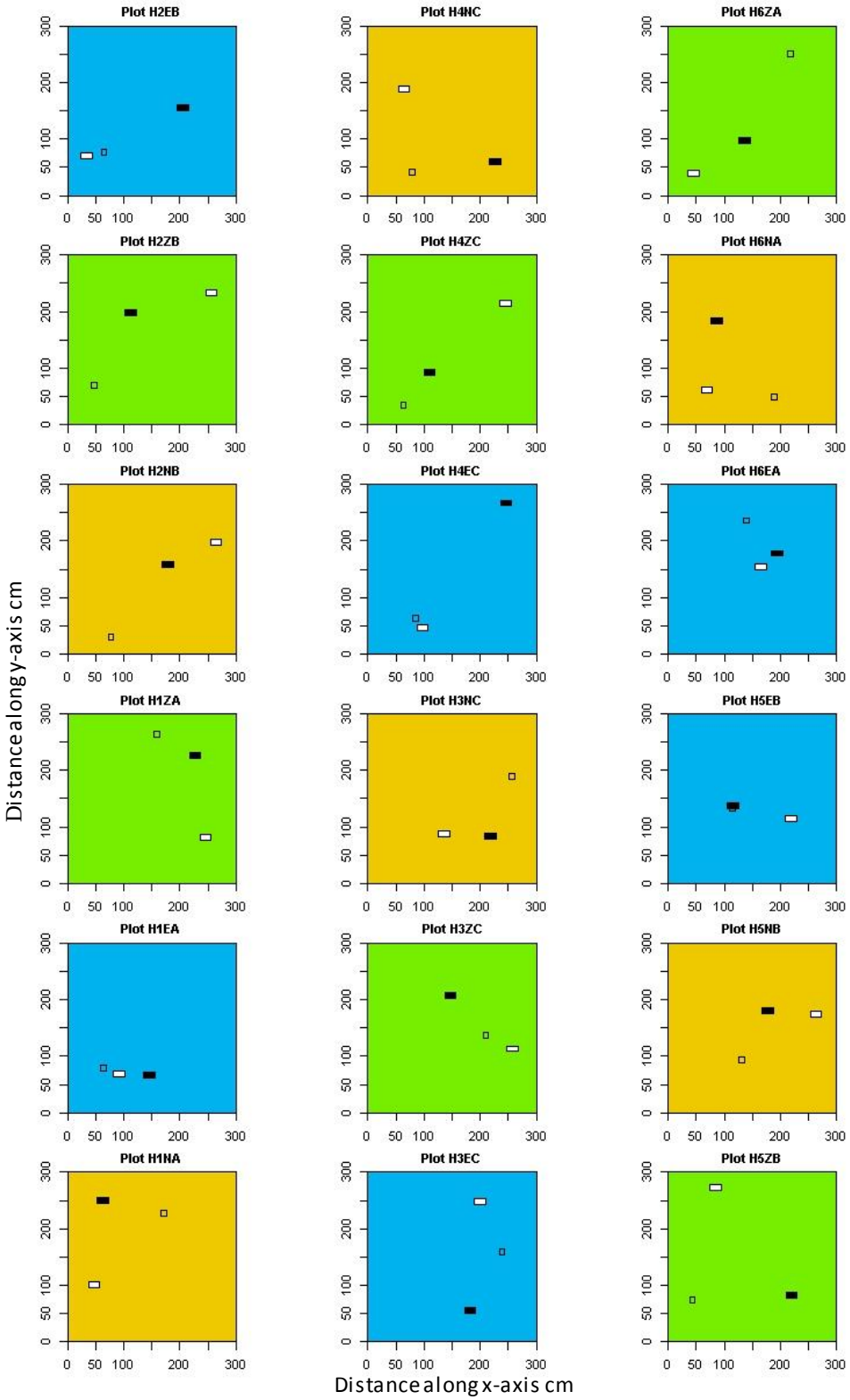

Figure 2. Howard's Field position of litter bags and bait lamina strips in the RHS experimental plots: black rectangles: twig litter bags, white rectangles: leaf litter bags, unfilled squares: bait lamina strips. Yellow: Native plots, green: Near native plots and blue: Exotic plots.

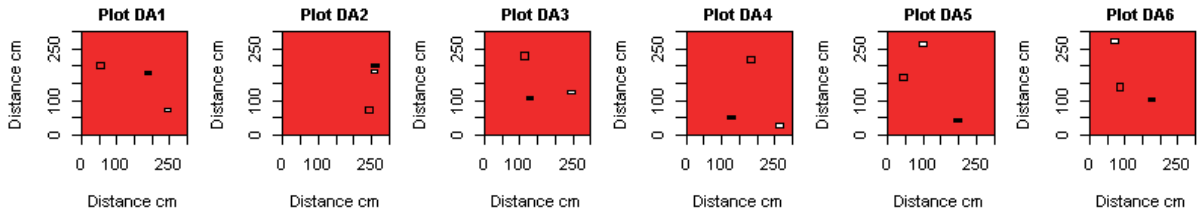

Figure 3. Deer's Farm Adjacent plots position of litter bags and bait lamina strips: black rectangles: twig litter bags, white rectangles: leaf litter bags, unfilled squares: bait lamina strips.

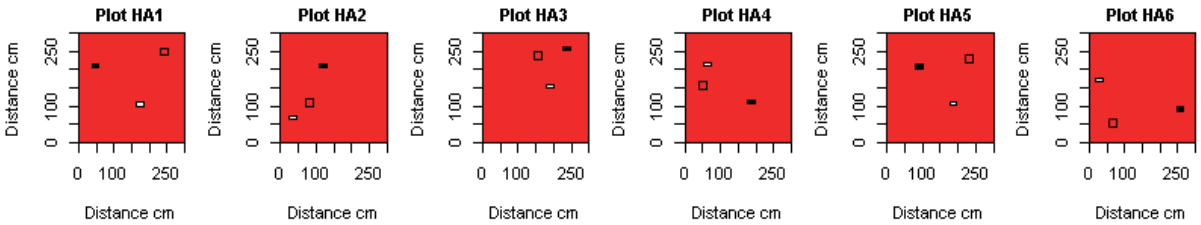

Figure 4. Howard's Field Adjacent plots position of litter bags and bait lamina strips: black rectangles: twig litter bags, white rectangles: leaf litter bags, unfilled squares: bait lamina strips.

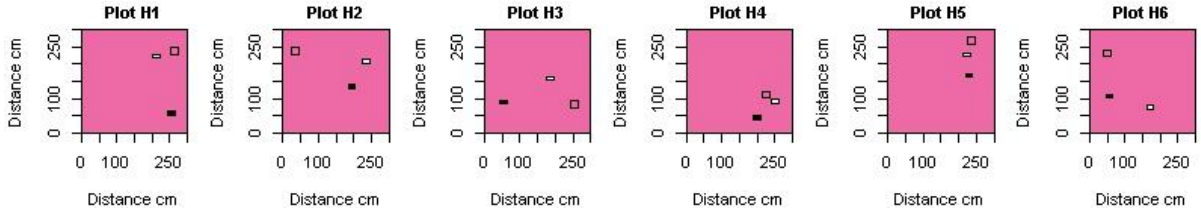

Figure 5. Wisley Common plots position of litter bags and bait lamina strips: black rectangles: twig litter bags, white rectangles: leaf litter bags, unfilled squares: bait lamina strips.

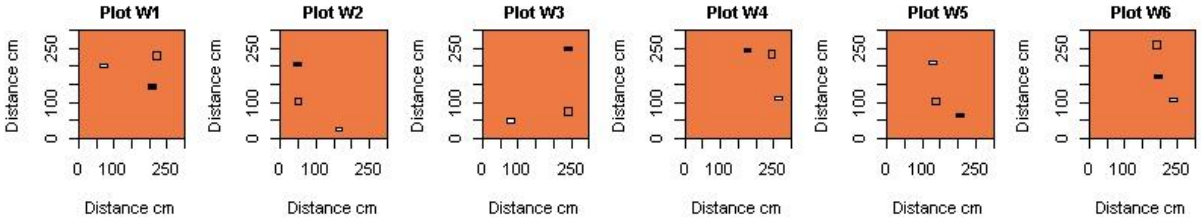

Figure 6. Buxton Wood plots position of litter bags and bait lamina strips: black rectangles: twig litter bags, white rectangles: leaf litter bags, unfilled squares: bait lamina strips.

Figure 7. Bait lamina strips prior to insertion end being cut to a point.

Appendix 5.4.1.

Table 1. *Q. robur* leaf litter bags initial dry mass (g) and final dry mass (g) after burial for 6.5 months (to 2 d.p.).

		Litter bag 1		Litter bag 2	
Site/treatment	**Plot**	**Initial**	**Final**	**Initial**	**Final**
Deer's N	D5NB	2.02	1.43	2.02	1.33
	D3NA	2.02	0.93	2.02	0.82
	D1NB	2.02	1.03	2.02	1.11
	D2NC	2.02	0.83	2.02	1.21
	D6NC	2.02	1.27	2.02	1.69
	D4NA	2.02	1.39	2.02	1.56
Deer's Z	D1ZB	2.02	1.26	2.02	1.14
	D3ZA	2.02	0.52	2.02	1.62
	D5ZB	2.02	1.20	2.02	1.09
	D2ZC	2.02	0.97	2.02	0.57
	D4ZA	2.02	0.92	2.02	1.63
	D6ZC	2.02	0.95	2.02	1.41
Deer's E	D1EB	2.02	0.89	2.02	1.24
	D3EA	2.02	1.21	2.02	1.47
	D5EB	2.02	1.56	2.02	1.42
	D6EC	2.02	0.41	2.02	0.41
	D4EA	2.02	1.02	2.02	1.10
	D2EC	2.02	1.37	2.02	1.49
Howard's N	H1NA	2.02	0.64	2.02	1.20
	H5NB	2.02	0.46	2.02	0.55
	H3NC	2.02	0.90	2.02	1.17
	H2NB	2.02	1.04	2.02	1.21
	H6NA	2.02	0.59	2.02	1.43
	H4NC	2.02	1.36	2.02	1.32
Howard's Z	H5ZB	2.02	0.96	2.02	1.29
	H3ZC	2.02	1.10	2.02	0.98
	H1ZA	2.02	1.32	2.02	1.43
	H2ZB	2.02	1.21	2.02	0.93
	H4ZC	2.02	1.42	2.02	1.21
	H6ZA	2.02	1.38	2.02	1.52
Howard's E	H3EC	2.02	1.29	2.02	1.30
	H1EA	2.02	1.15	2.02	1.39
	H5EB	2.02	1.20	2.02	1.37
	H6EA	2.02	1.37	2.02	1.55
	H4EC	2.02	1.30	2.02	1.47
	H2EB	2.02	1.39	2.02	1.42
Deer's A	DA1	2.02	1.80	2.02	1.95
	DA2	2.02	1.92	2.02	1.80
	DA3	2.02	1.83	2.02	1.90
	DA4	2.02	1.78	2.02	1.88
	DA5	2.02	1.98	2.02	1.81

	DA6	2.02	1.80	2.02	1.88
Howard's A	HA1	2.02	1.52	2.02	1.53
	HA2	2.02	1.55	2.02	1.62
	HA3	2.02	1.61	2.02	1.48
	HA4	2.02	1.56	2.02	1.51
	HA5	2.02	1.52	2.02	1.67
	HA6	2.02	1.56	2.02	1.52
Wisley Common	H1	2.02	1.54	2.02	1.53
	H2	2.02	1.63	2.02	1.56
	H3	2.02	1.81	2.02	1.66
	H4	2.02	1.37	2.02	1.48
	H5	2.02	1.61	2.02	1.59
	H6	2.02	1.45	2.02	1.67
Buxton Wood	W1	2.02	1.42	2.02	1.32
	W2	2.02	1.46	2.02	1.27
	W3	2.02	1.54	2.02	1.39
	W4	2.02	1.54	2.02	1.47
	W5	2.02	1.67	2.02	1.66
	W6	2.02	1.36	2.02	1.42

Table 2. Full results of the two-way ANOVA (AOV) on the percentage dry mass lost of *Q. robur* leaves after 6.5 months burial with RHS experimental site and planting treatment as factors. Site: Deer's Farm, Howards Field. Treatment: Native, Near native, Exotic, and the Kruskal-Wallis (K-W) with the three planting treatments.

Test	Factor	F value	X^2 value	d.f.	p value	significance
AOV	Treatment	0.917	NA	2	0.411	NS
	Site	0.210	NA	1	0.650	NS
	Site:Treatment	2.650	NA	2	0.087	NS
K-W	Treatment	NA	3.163	2	0.206	NS

Table 3. Tukey's HSD post-hoc test results: p values for multiple comparisons of percentage mass lost of *Q. robur* leaves between sites. DF: Deer's Farm RHS experimental plots, HF: Howard's Field RHS experimental plots, DFA: Deer's Farm adjacent, HFA: Howard's Field adjacent, H: Wisley Common, W: Buxton Wood.

	HF	DF	DFA	HFA	H
DF	**p > 0.05**				
DFA	**p < 0.001 *** **	**p < 0.001 *** **			
HFA	**p < 0.01 ** **	**p < 0.001 *** **	**p > 0.05**		
H	**p < 0.01 ** **	**p < 0.01 ** **	**p > 0.05**	**p > 0.05**	
W	**p > 0.05**	**p < 0.05 * **	**p < 0.05 * **	**p > 0.05**	**p > 0.05**

NS: p > 0.05, *: p < 0.05, **: p < 0.01, ***: p < 0.001

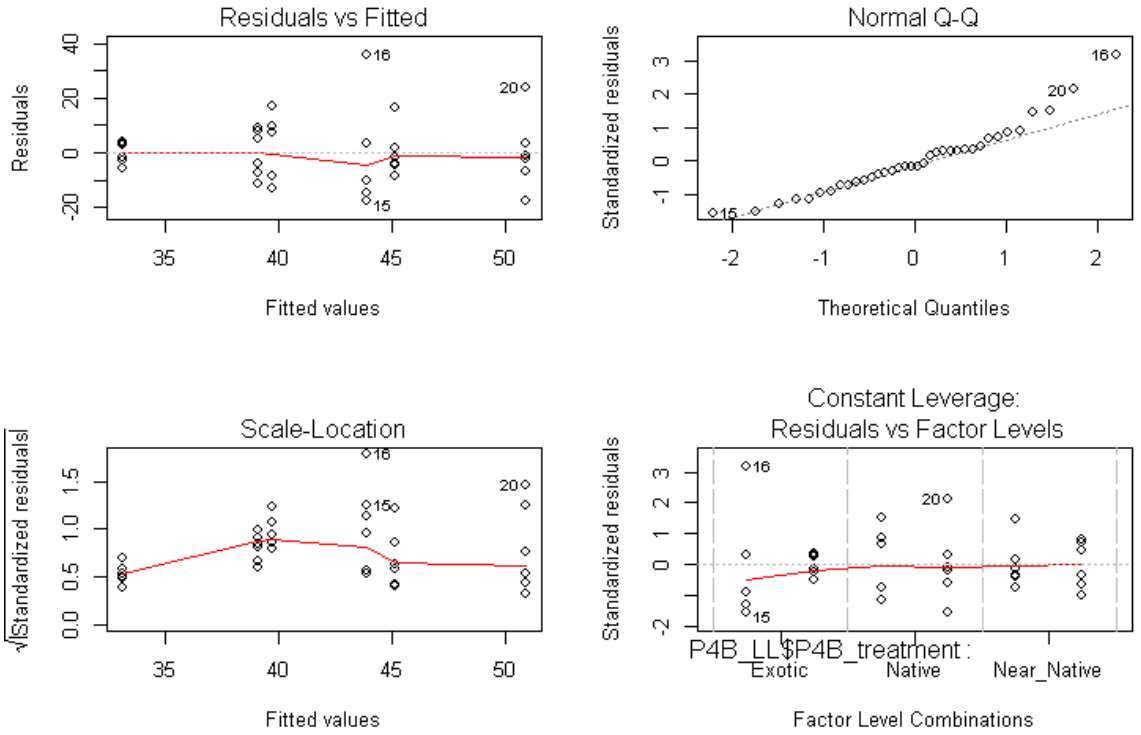

Figure 1. Plots of residuals for the two-way ANOVA on percentage dry mass lost of *Q. robur* leaves after 6.5 months burial with RHS experimental site and treatment as factors.

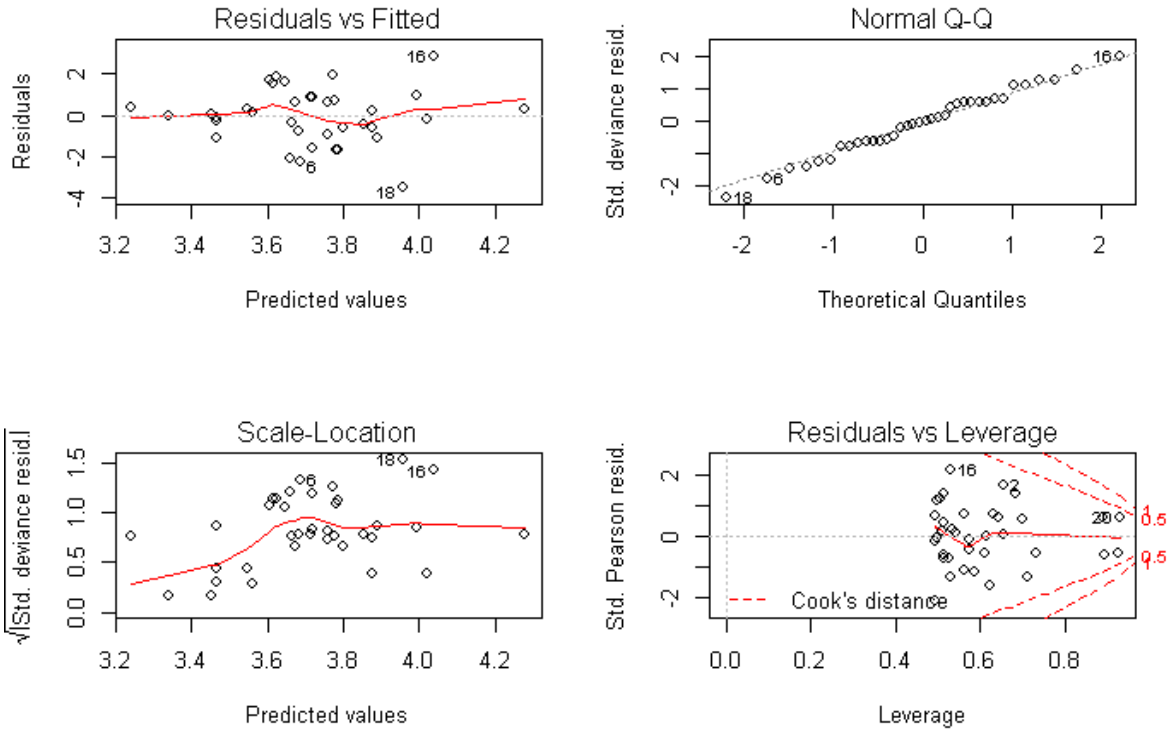

Figure 2. Plots of residuals for the global starting model of *Q. robur* percentage dry mass lost from leaf litter bags after 6.5 months, for the RHS experimental plot data, prior to stepwise deletion of non-significant terms; adjusted $R^2 = 0.9989$.

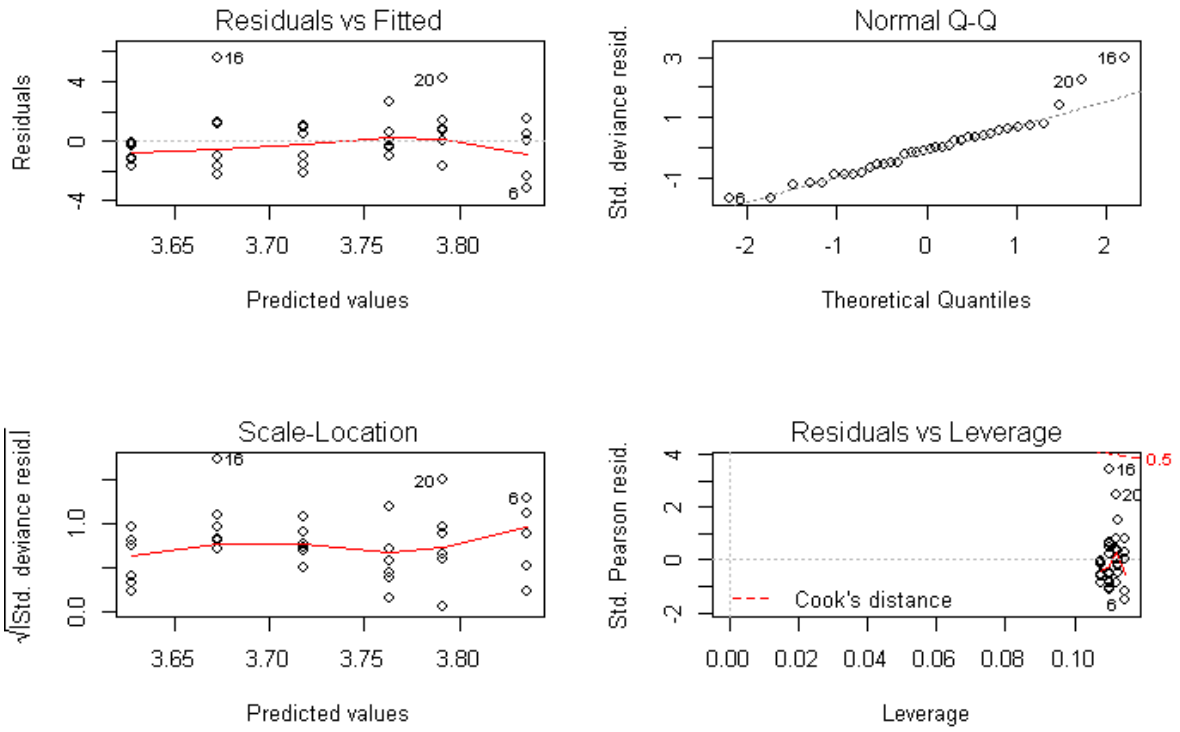

Figure 3. Plots of residuals for the generalised linear model of *Q. robur* percentage dry mass lost from leaf litter bags after 6.5 months, for the RHS experimental plot data, after stepwise deletion of non-significant terms until only 'site' and treatment remained; adjusted $R^2 = 0.9893$.

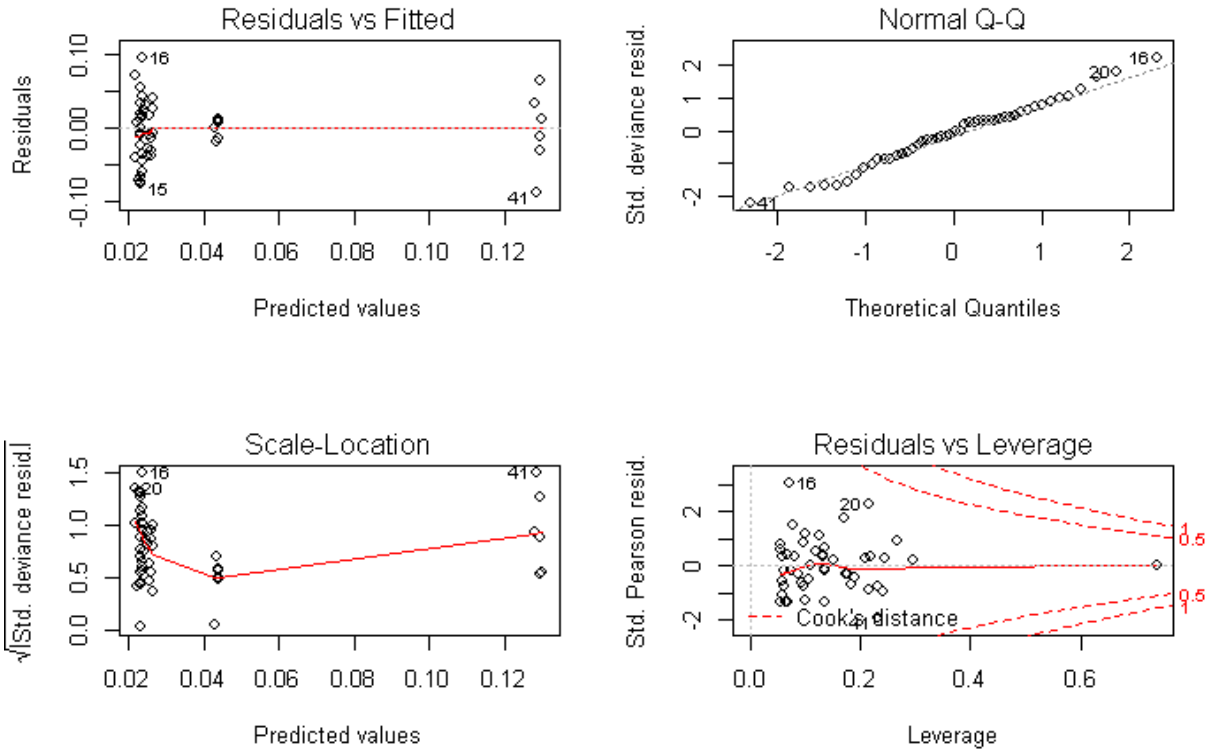

Figure 4. Plots of residuals for the global starting model of *Q. robur* percentage dry mass lost from leaf litter bags after 6.5 months, for the RHS experimental plot and adjacent grassland data, prior to stepwise deletion of non-significant terms; AIC = 338.85 , adjusted $R^2 = 1$ (non-transformed data).

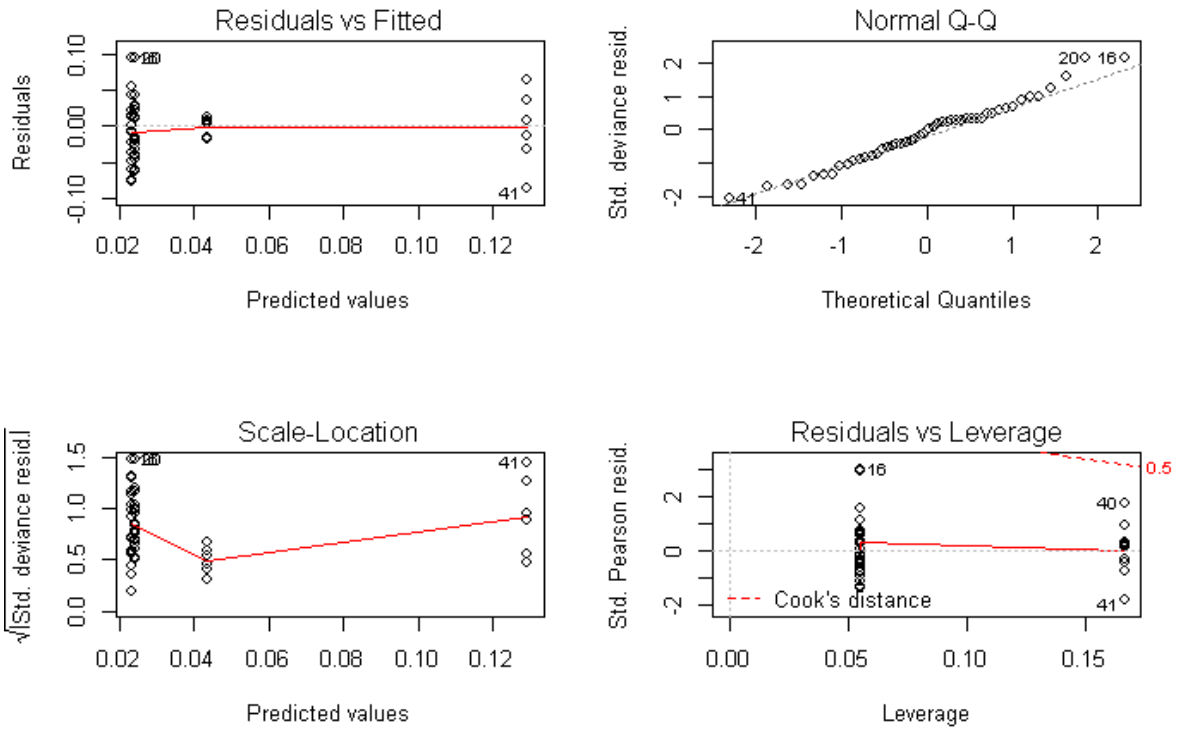

Figure 5. Plots of residuals for the global starting model of *Q. robur* percentage dry mass lost from leaf litter bags after 6.5 months, for the RHS experimental plot and adjacent grassland data, after stepwise deletion of non-significant terms; AIC = 334.15, adjusted $R^2 = 1$ (non-transformed data).

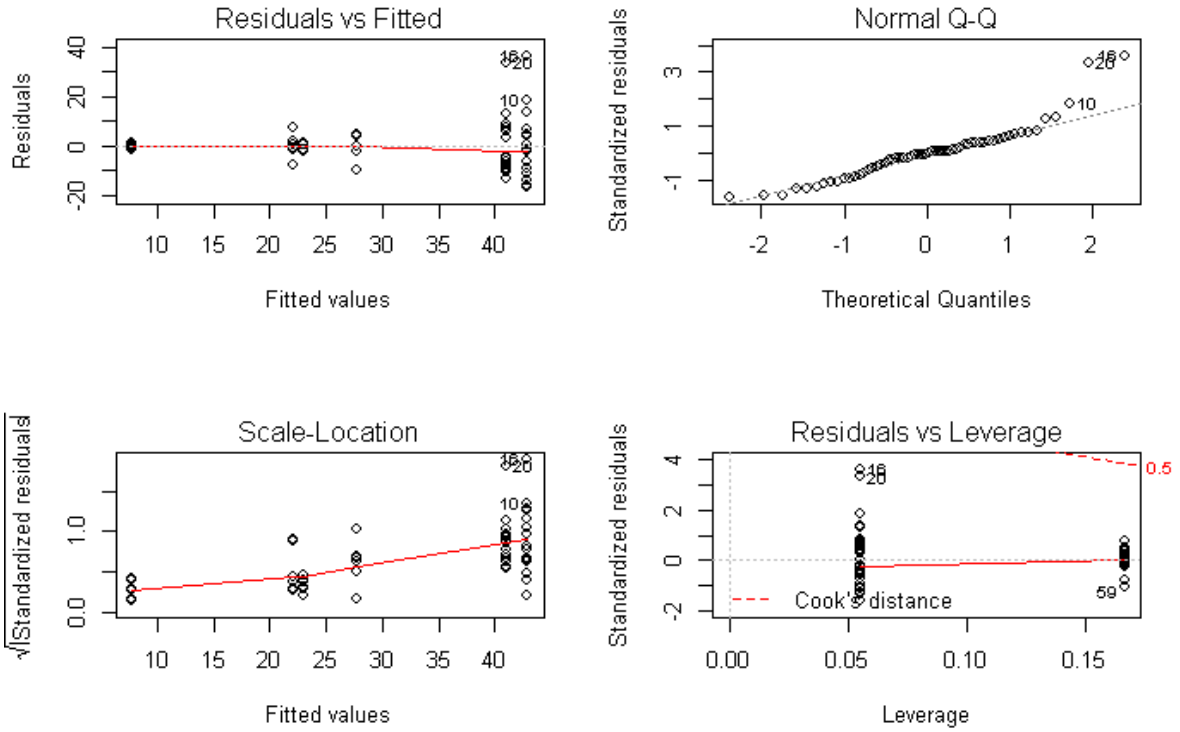

Figure 6. Plots of residuals for the one-way ANOVA on percentage dry mass lost from *Q. robur* leaf litter bags, from all sites, with 'Sithab' as the independent variable.

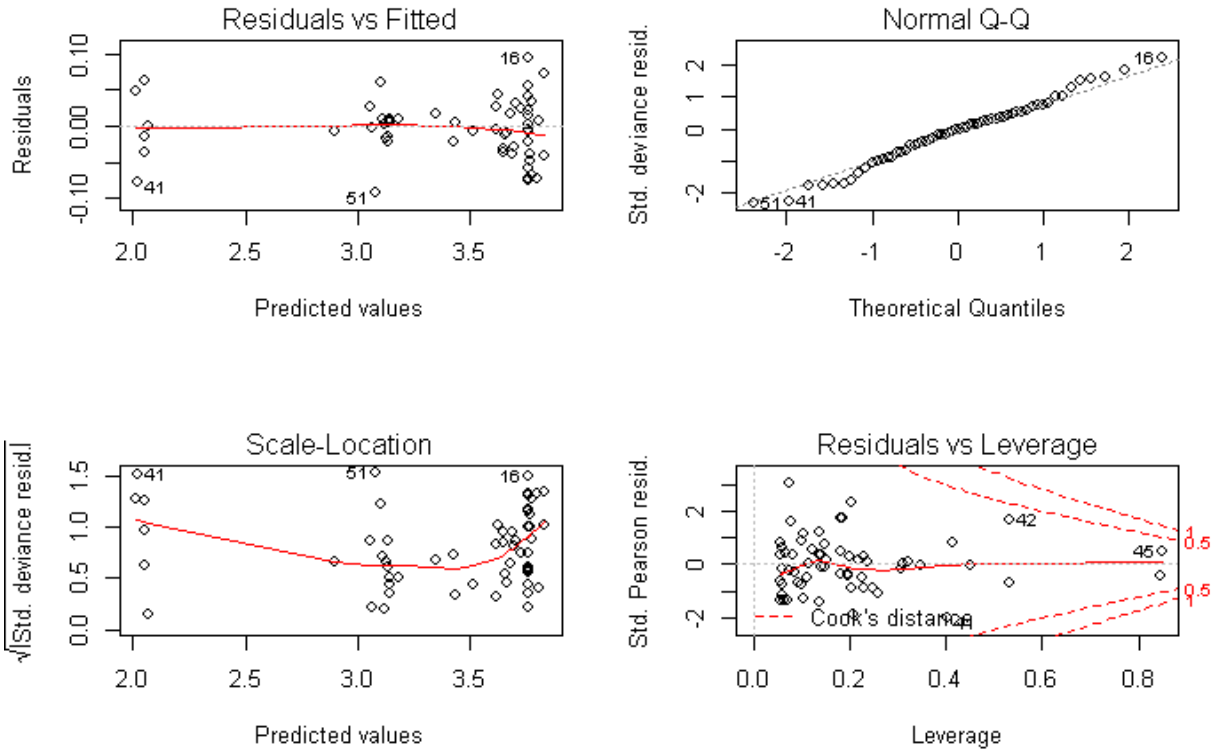

Figure 7. Plots of residuals for the global starting model of *Q. robur* percentage dry mass lost from leaf litter bags after 6.5 months, all sites, prior to stepwise deletion of non-significant terms; AIC = 416.95 , adjusted R^2 = 0.9998 (non-transformed data).

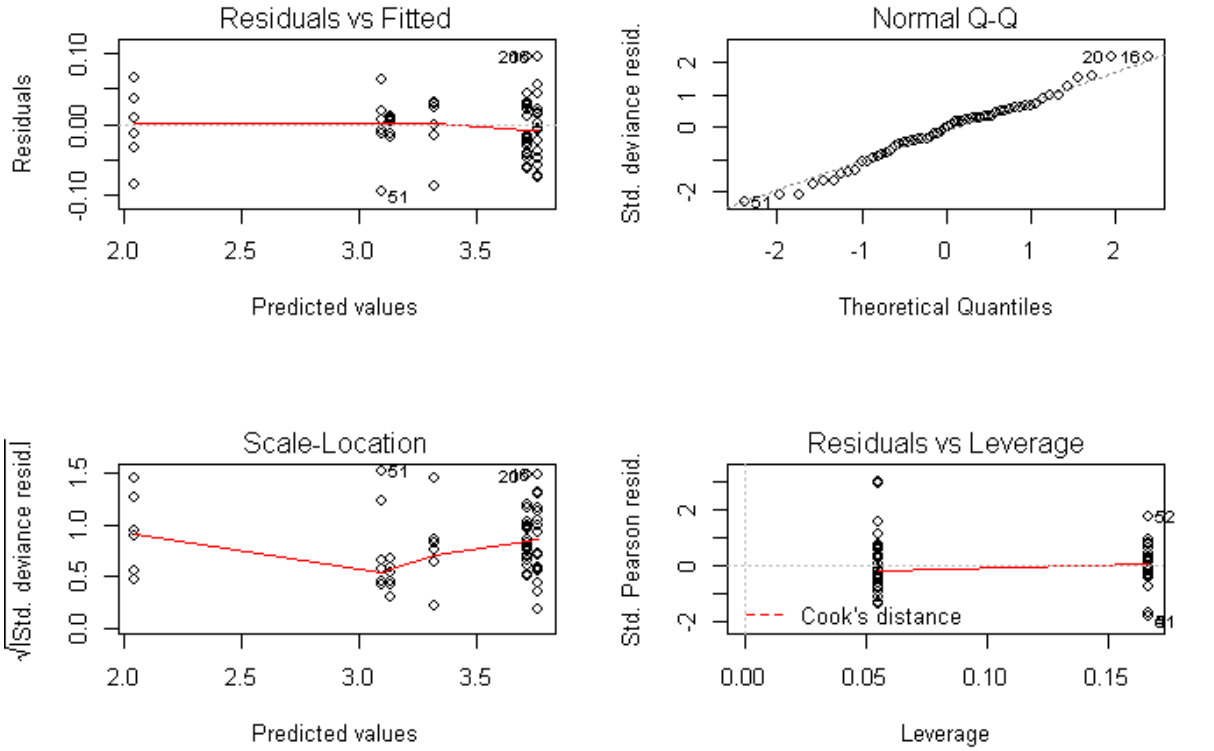

Figure 8. Plots of residuals for the global starting model of *Q. robur* percentage dry mass lost from leaf litter bags after 6.5 months, all sites, after stepwise deletion of non-significant terms; AIC = 412.07 , adjusted R^2 = 0.9998 (non-transformed data).

Appendix 5.4.2.

Table 1. Decay constants of (k) *B. pendula* twig litter bags buried for half a year, 1 year, 1.5 years and 2 years ± standard error of the mean.

Site	Treatment	k (0.5 year)	k (1 year)	k (1.5 years)	k (2 years)
Deer's Farm	**Native**	0.789 ± 0.025	0.768 ± 0.071	0.819 ± 0.040	0.677 ± 0.075
	Near native	0.895 ± 0.050	1.097 ± 0.124	0.828 ± 0.115	0.657 ± 0.075
	Exotic	0.765 ± 0.112	0.759 ± 0.085	0.807 ± 0.091	0.730 ± 0.020
	Adjacent	1.184 ± 0.183	0.587 ± 0.030	1.110 ± 0.267	0.454 ± 0.026
Howard's Field	**Native**	0.834 ± 0.038	0.420 ± 0.008	0.750 ± 0.034	0.338 ± 0.066
	Near native	0.918 ± 0.039	0.381 ± 0.021	0.745 ± 0.030	0.502 ± 0.100
	Exotic	0.954 ± 0.104	0.760 ± 0.032	0.755 ± 0.118	0.667 ± 0.032
	Adjacent	1.055 ± 0.161	0.725 ± 0.061	0.872 ± 0.090	0.597 ± 0.029
Wisley Common		0.940 ± 0.047	0.691 ± 0.082	0.864 ± 0.053	0.545 ± 0.035
Buxton Wood		0.753 ± 0.056	0.790 ± 0.086	0.798 ± 0.120	0.563 ± 0.055

Table 2. Results of linear regression models of the percentage dry mass remaining of *B. pendula* twigs.

Site	Treatment	R^2	adj R^2	d.f.	Error d.f.	p value	Decay gradient
Deer's Farm	**Native**	0.650	0.634	1	22	$p < 0.001$	-0.103
	Near native	0.703	0.690	1	22	$p < 0.001$	-0.093
	Exotic	0.776	0.764	1	19	$p < 0.001$	-0.091
	RHS site	0.697	0.692	1	67	$p < 0.001$	-0.096
	Adjacent	0.790	0.775	1	14	$p < 0.001$	-0.020
Howard's Field	**Native**	0.749	0.737	1	22	$p < 0.001$	-0.065
	Near native	0.550	0.525	1	18	$p < 0.001$	-0.097
	Exotic	0.748	0.736	1	22	$p < 0.001$	-0.075
	RHS site	0.615	0.609	1	66	$p < 0.001$	-0.078
	Adjacent	0.675	0.657	1	18	$p < 0.001$	-0.048
Wisley Common		0.385	0.355	1	21	$p < 0.01$	-0.033
Buxton Wood		0.804	0.795	1	22	$p < 0.001$	-0.043

Table 3. Results of the second order polynomial regression models of the percentage dry mass remaining of *B. pendula* twigs for each treatment and site.

Site	Treatment	R^2	adj R^2	d.f.	Error d.f.	p value
Deer's Farm	**Native**	0.852	0.838	2	21	p < 0.001
	Near native	0.826	0.810	2	21	p < 0.001
	Exotic	0.924	0.916	2	18	p < 0.001
	RHS site	0.851	0.846	2	66	p < 0.001
	Adjacent	0.801	0.771	2	13	p < 0.001
Howard's Field	**Native**	0.841	0.826	2	21	p < 0.001
	Near native	0.700	0.665	2	17	p < 0.001
	Exotic	0.860	0.846	2	21	p < 0.001
	RHS site	0.793	0.789	2	65	p < 0.001
	Adjacent	0.730	0.699	2	17	p < 0.001
Wisley Common		0.548	0.501	2	20	p < 0.001
Buxton Wood		0.871	0.859	2	21	p < 0.001

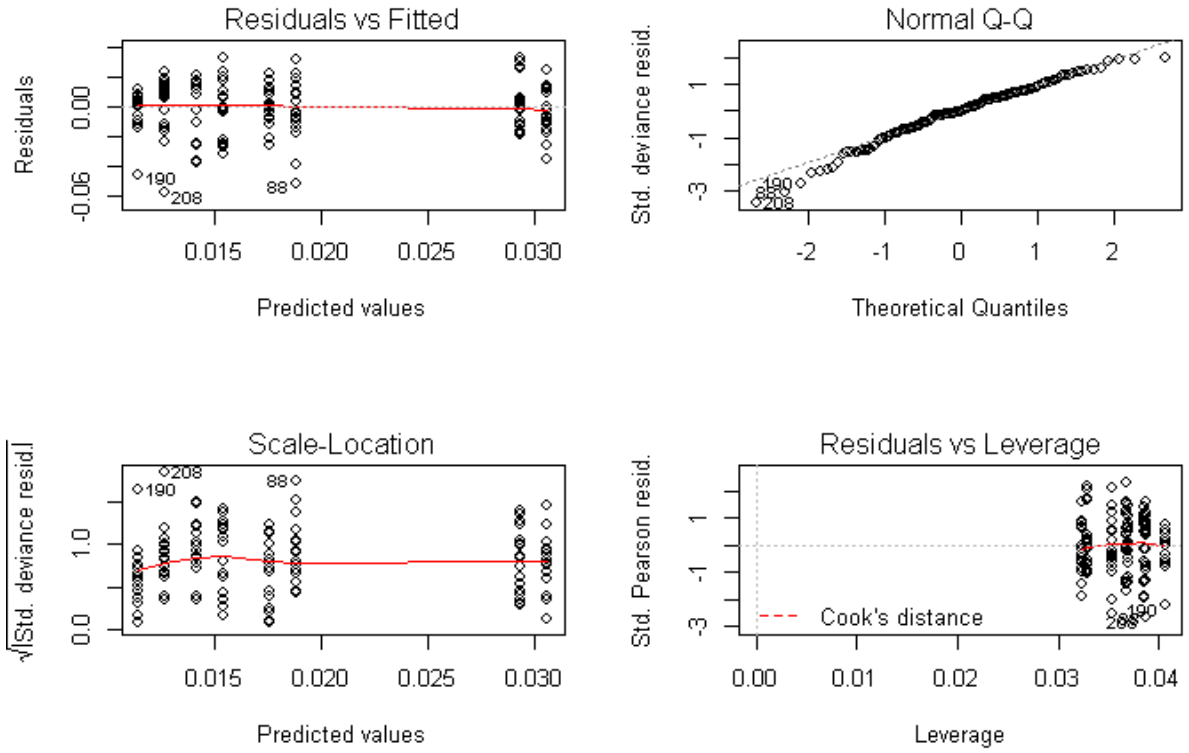

Figure 1. Plots of residuals for the final model of *B. pendula* percentage dry mass lost from twig litter bags, for the RHS experimental plot data, after stepwise deletion of non-significant terms; adjusted $R^2 = 1$, AIC = 944.19.

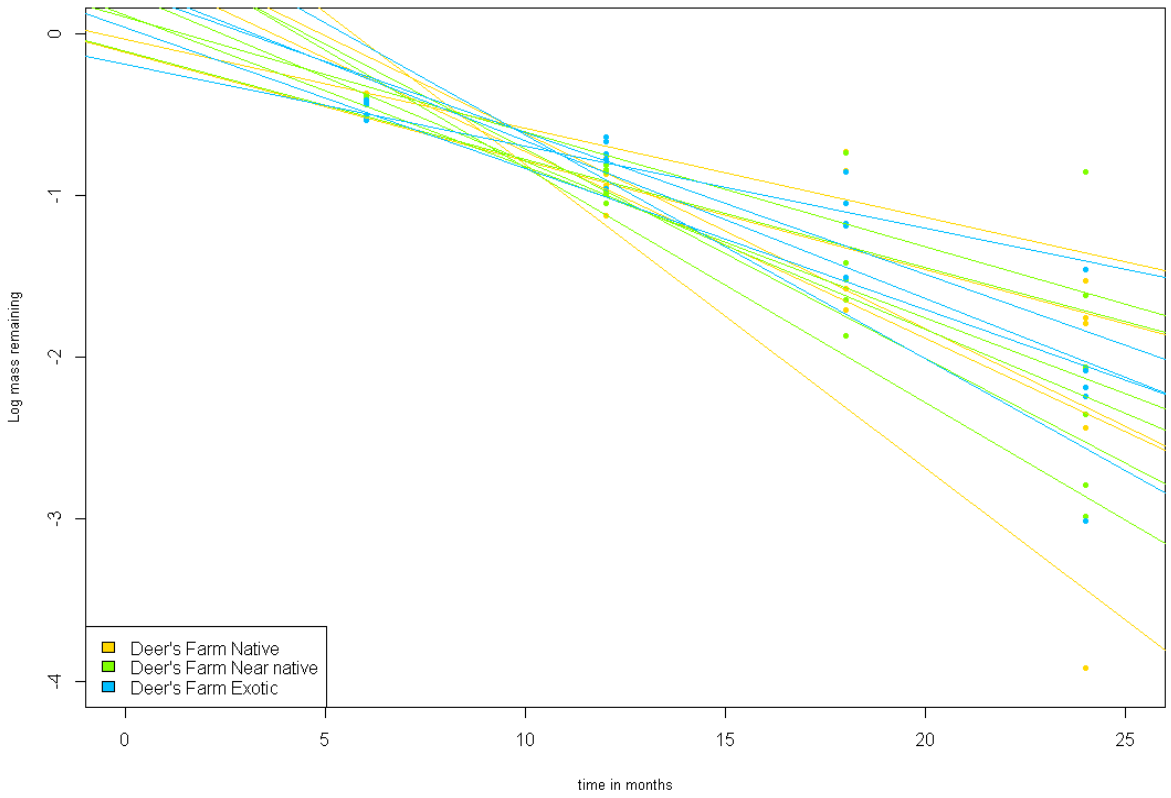

Figure 2. Linear regressions of Log (percentage mass remaining/100) of *B. pendula* twig litter bags after 6, 12, 18 and 24 months under each plot for three vegetation origin treatments at the Deer's Farm RHS experimental site. Native: yellow, Near native: green, Exotic: blue. See Table 2. for the R^2 and p values.

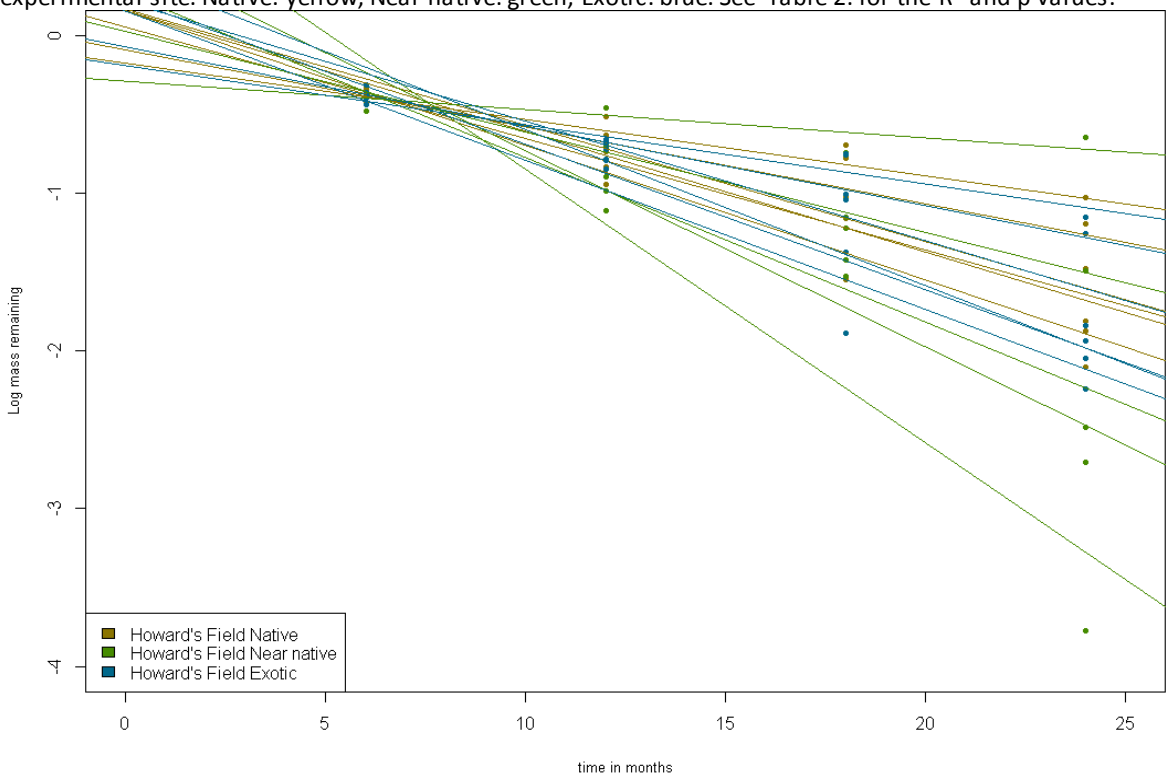

Figure 3. Linear regressions of Log (percentage mass remaining/100) of *B. pendula* twig litter bags after 6, 12, 18 and 24 months under each plot for three vegetation origin treatments at the Howard's Farm RHS experimental site. Native: yellow, Near native: green, Exotic: blue. See Table 2. for the R^2 and p values.

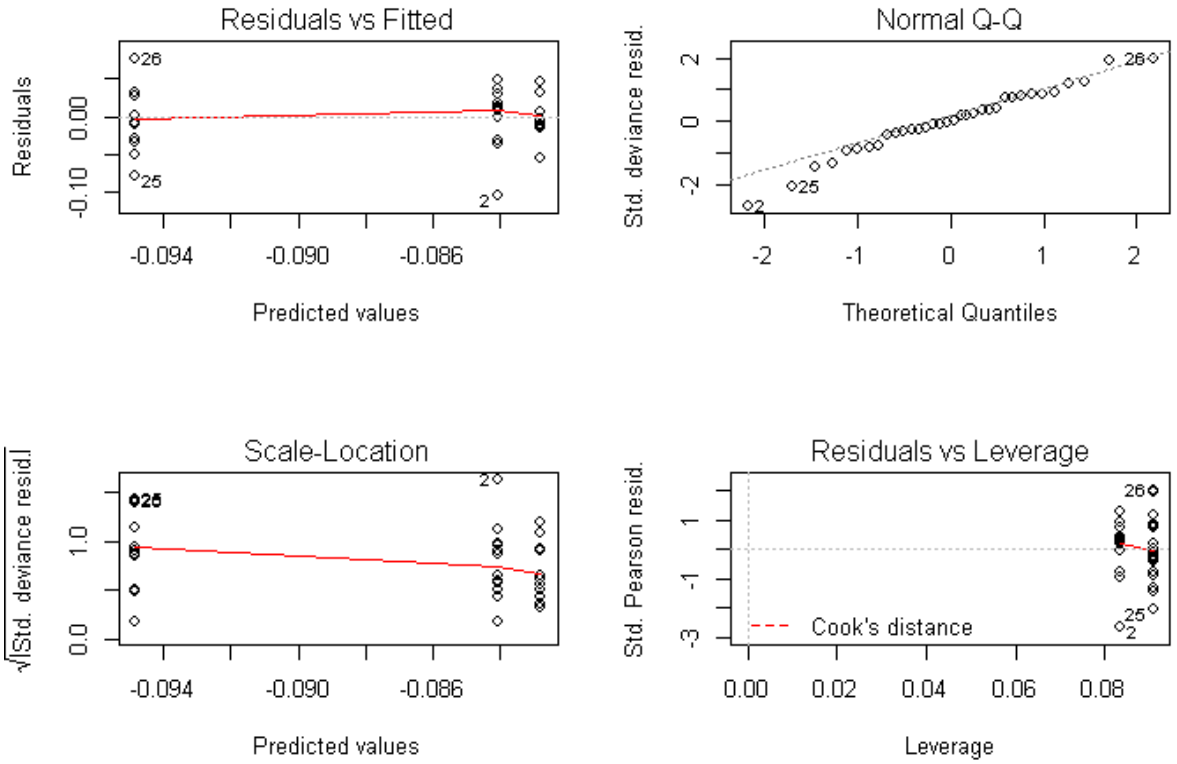

Figure 4. Plots of residuals for the final model of *B. pendula* decomposition rates, for the RHS experimental plot data, after stepwise deletion of non-significant terms; adjusted R^2 = -0.04436, AIC = -116.85.

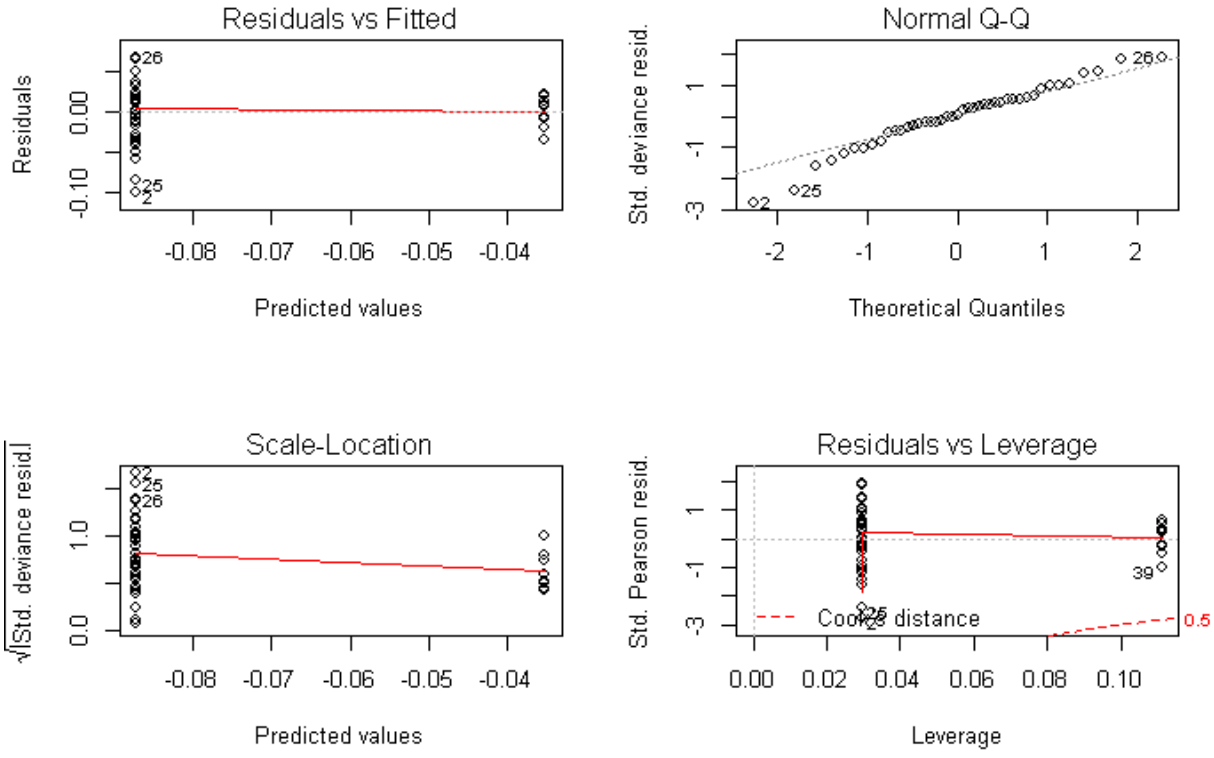

Figure 5. Plots of residuals for the final model of *B. pendula* decomposition rates, for the RHS experimental plot and adjacent grassland data, after stepwise deletion of non-significant terms; adjusted R^2 = 0.2421, AIC = -158.92.

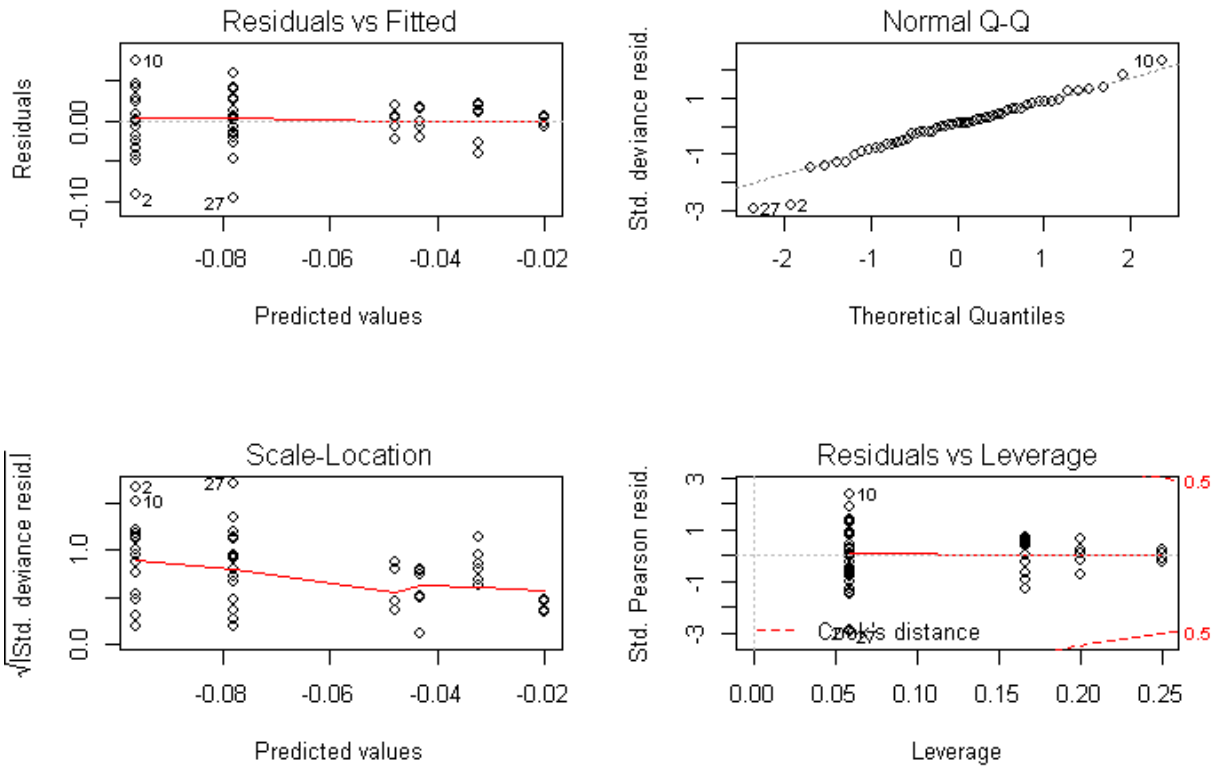

Figure 6. Plots of residuals for the final model of *B. pendula* decomposition rates, for all sites, after stepwise deletion of non-significant terms; adjusted R^2 = 0.3515, AIC = -210.41.

Appendix 5.4.3.

Table 1. Mean percentage bait consumed, from bait lamina strips, per treatment after 5, 8, 11, 20, 32 and 54 days.

Site	Treatment	5 days	8 days	11 days	14 days	20 days	32 days	54 days
Deer's Farm	**Native**	2%	6%	8%	14%	13%	30%	57%
	Near native	5%	7%	13%	16%	18%	33%	53%
	Exotic	3%	5%	8%	10%	15%	32%	58%
	Adjacent	5%	8%	9%	13%	19%	24%	24%
Howard's Field	**Native**	5%	6%	13%	15%	21%	33%	47%
	Near native	5%	7%	11%	17%	26%	38%	61%
	Exotic	4%	7%	13%	17%	20%	33%	42%
	Adjacent	2%	2%	4%	4%	8%	13%	24%
Wisley Common		4%	4%	12%	15%	18%	25%	31%
Buxton Wood		11%	11%	13%	13%	16%	24%	31%

Table 2. Mean soil moisture content of each plot (percentage volumetric water content).

	DFN	DFZ	DFE	HFN	HFZ	HFE	DFA	HFA	H	W
plot 1	4.2	8.8	14.7	10.9	7.8	9.0	4.4	8.1	8.2	25.7
plot 2	13.6	8.2	8.5	13.4	12.8	13.0	5.1	6.1	8.7	21.4
plot 3	11.0	2.0	9.2	7.3	7.7	11.8	2.8	7.1	22.4	28.3
plot 4	7.1	8.3	4.8	4.0	7.8	14.8	2.5	6.7	3.5	10.7
plot 5	3.2	14.0	6.8	7.8	7.7	4.9	2.6	5.4	12.8	20.7
plot 6	5.8	2.7	7.1	7.5	5.0	3.2	2.8	9.2	7.9	23.6
treatment mean	**7.5**	**7.3**	**8.5**	**8.5**	**8.1**	**9.4**	**3.4**	**7.1**	**10.6**	**21.7**
site mean		**7.8**			**8.7**		**3.4**	**7.1**	**10.6**	**21.7**

DFN = Deer's Farm Native, DFZ = Deer's Farm Near native, DFE = Deer's Farm Exotic, HFN = Howard's Field Native, HFZ = Howard's Field Near native, HFE = Howard's Field Exotic, DFA = Deer's Farm Adjacent, HFA = Howard's Field Adjacent, H = Wisley Common, W = Buxton Wood.

Table 3. Results of linear regression models of the percentage of bait lamina strip holes remaining filled under the different treatments/sites over 54 days.

Site	Treatment	adj R^2	d.f.	Error d.f.	p value	Rate of bait consumption
Deer's Farm	**Native**	0.765	1	40	p < 0.001	-0.017
	Near native	0.718	1	40	p < 0.001	-0.015
	Exotic	0.772	1	40	p < 0.001	-0.018
	RHS site	0.753	1	124	p < 0.001	-0.015
	Adjacent	0.596	1	40	p < 0.001	-0.004
Howard's Field	**Native**	0.320	1	40	p < 0.001	-0.013
	Near native	0.723	1	40	p < 0.001	-0.020
	Exotic	0.804	1	40	p < 0.001	-0.011
	RHS site	0.637	1	124	p < 0.001	-0.015
	Adjacent	0.598	1	40	p < 0.001	-0.006
Wisley Common		0.418	1	40	p < 0.001	-0.007
Buxton Wood		0.701	1	40	p < 0.001	-0.006

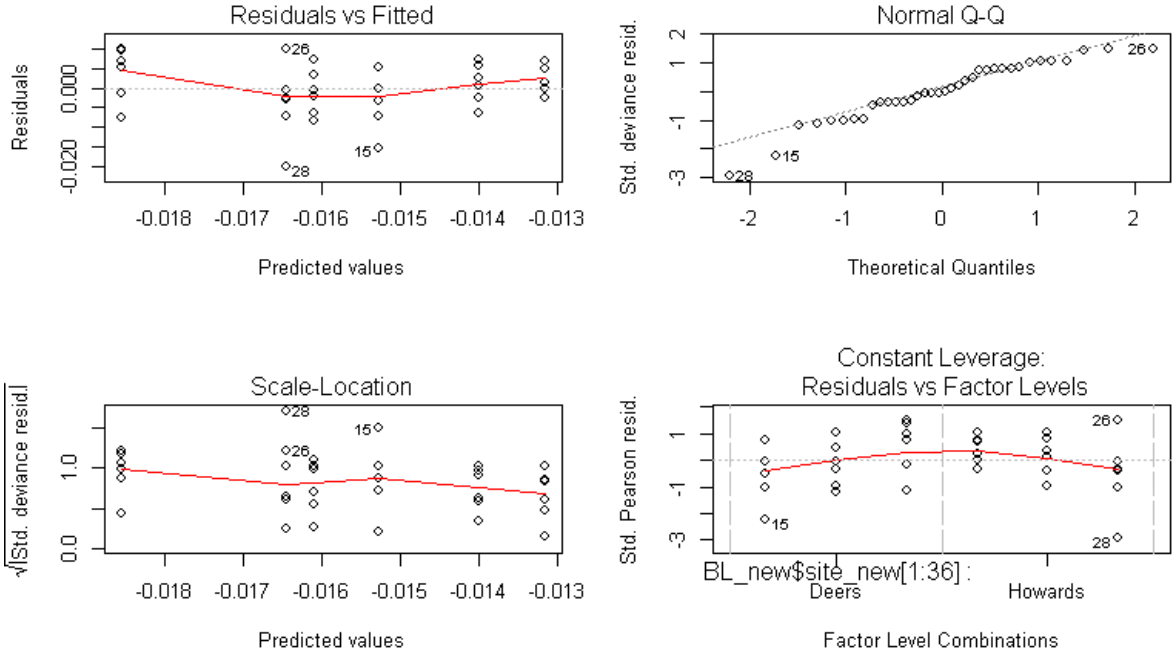

Figure 1. Plots of residuals for the final model of bait consumption, for the RHS experimental plot data, after stepwise deletion of non-significant terms; adjusted R^2 = -0.0271, AIC = -246.87.

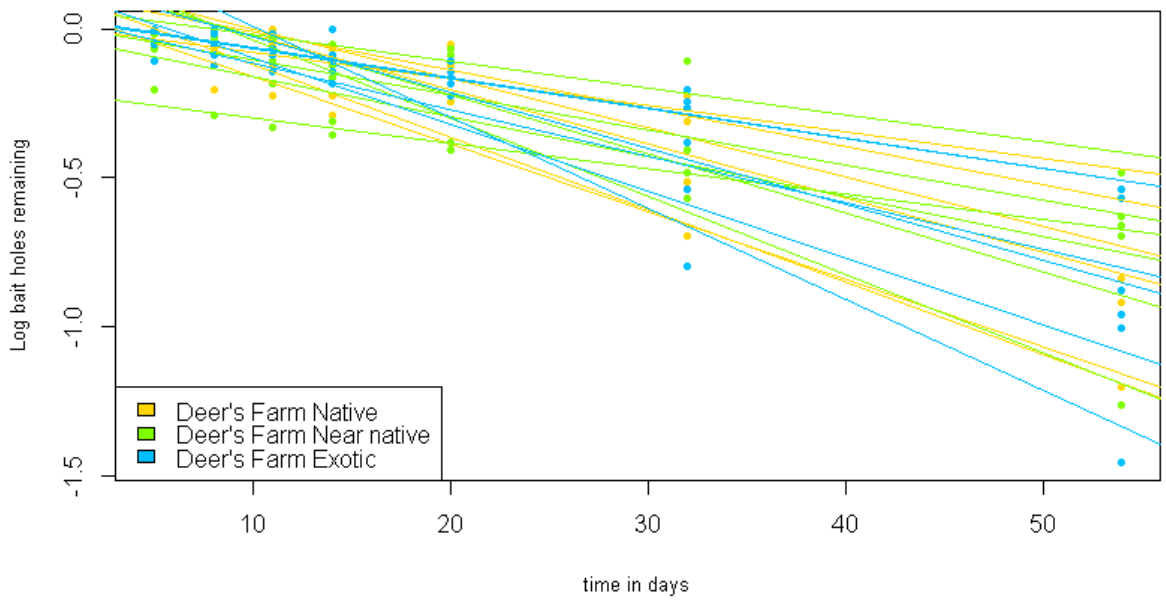

Figure 2. Linear regressions of Log (Linear regression of Log (percentage holes remaining filled/100) of bait lamina strips after 5, 8, 11, 20, 32 and 54 days, under each plot for three vegetation origin treatments at the Deer's Farm RHS experimental site. Native: yellow, Near native: green, Exotic: blue. See Table 2. for the R^2 and p values.

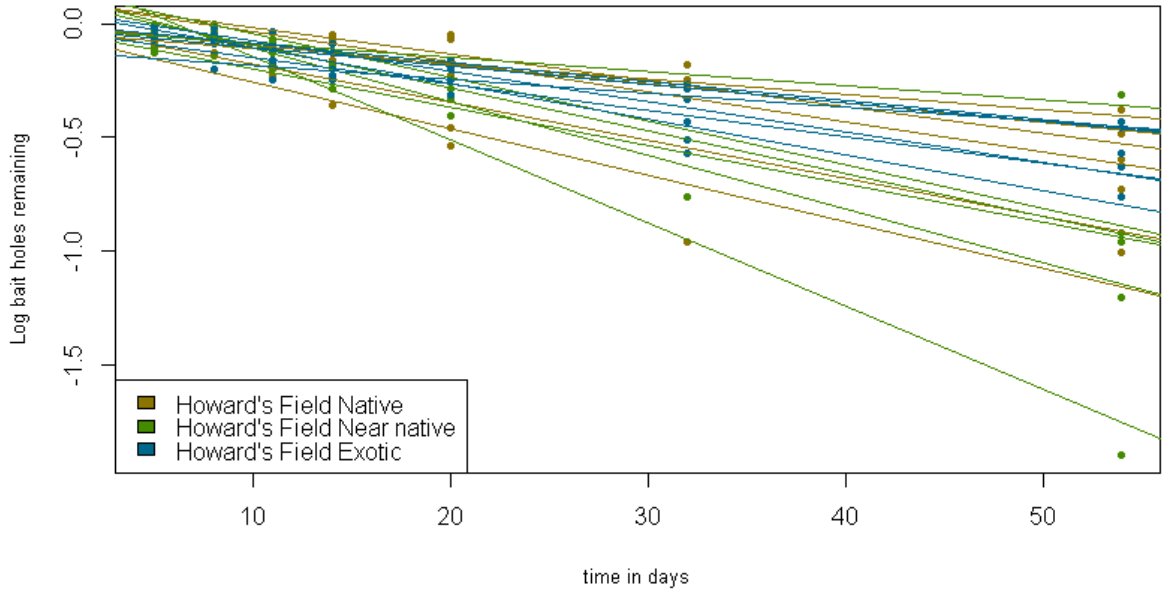

Figure 3. Linear regressions of Log (Linear regression of Log (percentage holes remaining filled/100) of bait lamina strips after 5, 8, 11, 20, 32 and 54 days, under each plot for three vegetation origin treatments at the Howard's Farm RHS experimental site. Native: yellow, Near native: green, Exotic: blue. See Table 2. for the R^2 and p values.

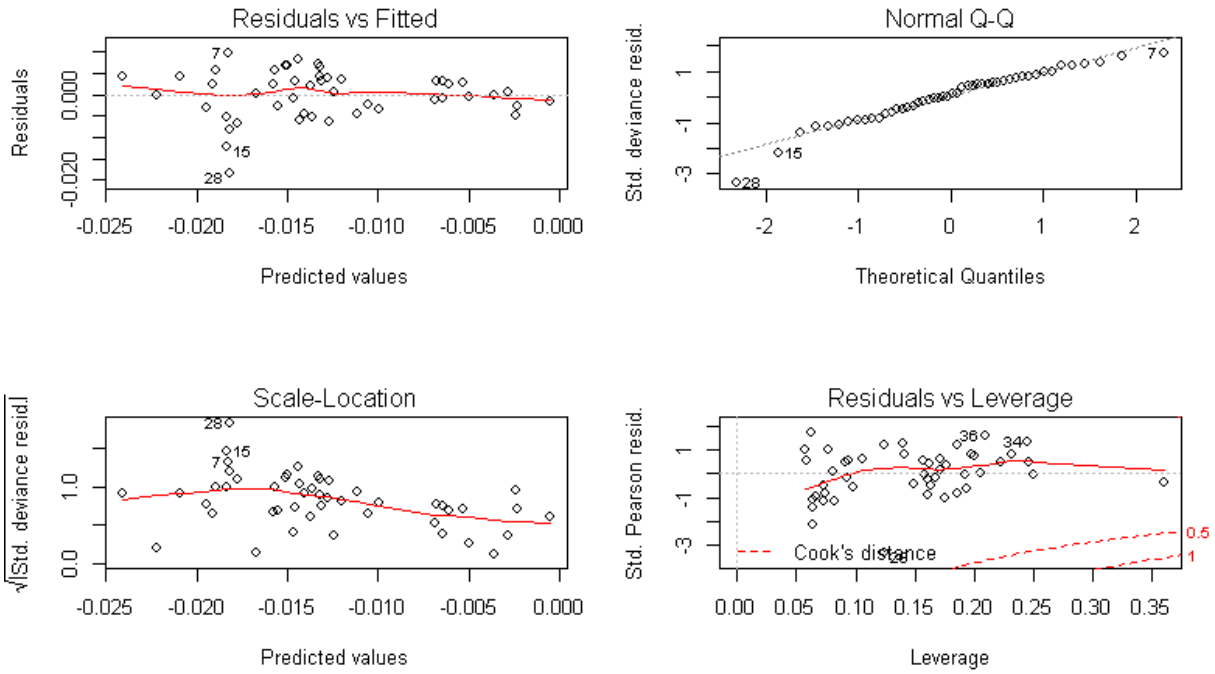

Figure 4. Plots of residuals for the final model of bait consumption, for the RHS experimental plot and adjacent grassland data, after stepwise deletion of non-significant terms; adjusted R^2 = 0451, AIC = -348.34.

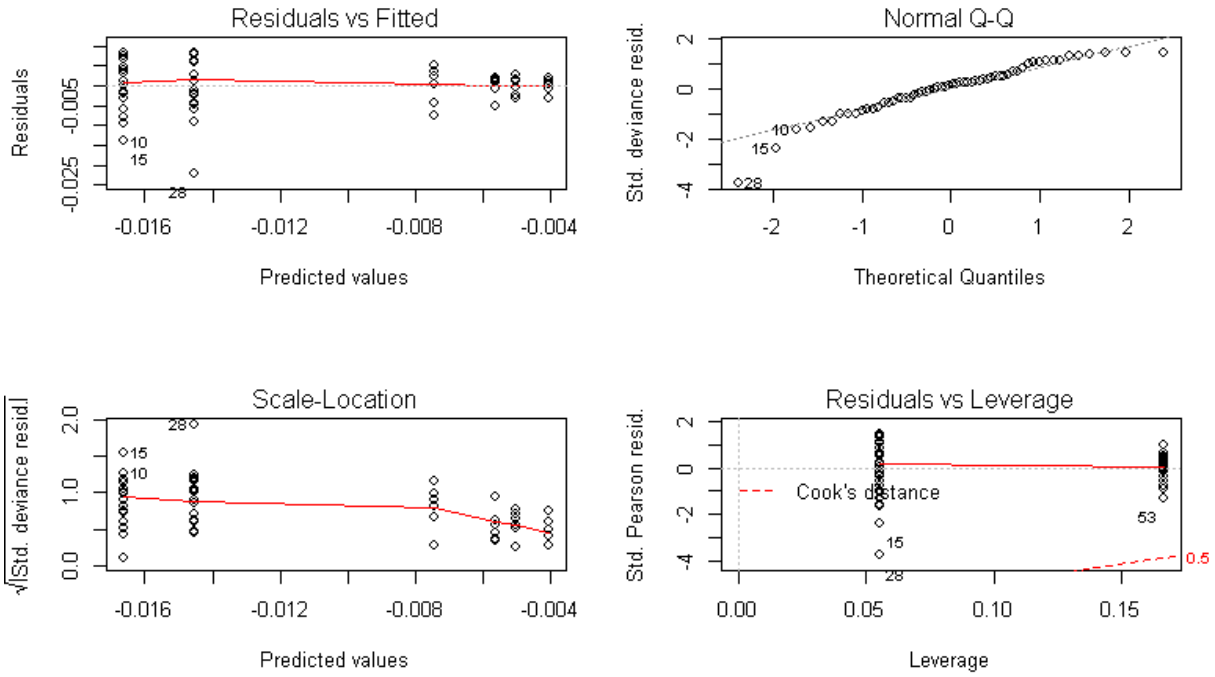

Figure 5. Plots of residuals for the final model of bait consumption, for all sites, after stepwise deletion of non-significant terms; adjusted R^2 = 0.3883, AIC = -435.93.

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